Proceedings of Symposium "Seed and Seedbed Ecology of Rangeland Plants"

(21-23 April 1987, Tucson, AZ)

Proceedings of Symposium "Seed and Seedbed Ecology of Rangeland Plants"

(21-23 April 1987, Tucson, AZ)

By
Gary W. Frasier
Raymond A. Evans

These Proceedings include all of the papers presented at the symposium "Seed and Seedbed Ecology of Rangeland Plants" held April 20-24, 1987 at Tucson, Arizona and sponsored by USDA-ARS, Aridland Watershed Management Research Unit, Tucson, Arizona. The purpose of the symposium was:

"To document the state of the science of seeding revegetation species on rangelands where seeding is done with limited or no seedbed preparation and seedling establishment is dependent on precipitation without supplemental irrigation."

The symposium consisted of 3 days of technical presentations with discussion periods in the evenings. A field trip to the USDA-ARS, Walnut Gulch Experimental Watershed, Tombstone, Arizona preceded the technical sessions. A second field trip to experimental revegetation study sites followed the technical sessions.

The symposium was co-chaired by Gary W. Frasier, USDA-ARS, Tucson, AZ and Raymond A. Evans, USDA-ARS (Retired), Reno, NV. Moderators for the technical sessions were: G. Fred Gifford, University of Nevada, Reno, Reno, NV; James McLaughlin, USDI-BLM, Reno, NV; James A. Young, USDA-ARS, Reno, NV; Dave Kathman, USDI-BLM, Denver, CO; and Howard Morton, USDA-ARS, Tucson, AZ. Featured luncheon speakers were: Robert F. Barnes, Executive Vice-President, ASA/CSSA/SSSA, Madison, WI; N.F.G. Rethman, University of Pretoria, Republic of South Africa; and Jorge Galo Medina T., Asesor de Rectoria, Universidad "Antonio Narro", Saltillo, Coahilla, Mexico. Luncheon chairmen were: Raymond A. Evans, USDA-ARS (Retired), Reno, NV; Jerry Cox, USDA-ARS, Tucson, AZ; and Gary Evans, USDA-ARS, Beltsville, MD. Gary Frasier, USDA-ARS, Tucson, AZ was the evening discussion leader.

The papers in this report are reproduced essentially as they were supplied by the authors. The opinions expressed are their own and do not necessarily reflect the views of the U. S. Department of Agriculture.

As the papers were prepared in reproducible form by the individual authors to expedite the publishing of the proceedings, there is some variation in type and format; however, such variations should not distract the attention of the reader. Queries regarding them should be referred to authors of the specific papers.

This camera copy was prepared and edited by Gary W. Frasier, Aridland Watershed Management Research Unit, 2000 East Allen Road, Tucson, Arizona 85719.

Copies of this publication may be purchased from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA. 22161.

ARS has no additional copies for free distribution.

412503

CONTENTS

THE SEED GERMINATION PROCESS

Gerald R. Leather[1]

ABSTRACT

Seed germination starts at the beginning of
imbibition and is completed at the onset of
radicle growth. The biochemical events specific
for germination have not been completely
defined, but are accomplished in three
identifiable phases associated with the uptake
and structure of water in the seed.

INTRODUCTION

The seed germination process encompasses a
myriad of events; some are well described and
understood while others are poorly defined or
are hypothesized. Bewley and Black (1978)
completed their brief discussion on the
germination process with: "No satisfactory
answer can therefore be given to the key
questions--what biochemical events are specific
to germination and how are they controlled?"
Some progress has been made to answer these
questions, but we cannot yet fully describe the
germination of a seed, linking all physical and
biochemical events. It would be a monumental
task to include in a brief summary all the
published research on seed germination, the
chemical and physical regulators of germination,
the biochemical processes involved, and the
events that may be different among species (for
reviews, Bewley and Black 1978, 1982; Khan 1982;
Murray 1984a, b). Thus, I will describe the
seed germination process in the simplest of
terms and confine my discussion to the topic of
most importance to this symposium--water.

The Mature Dry Seed

Beginning with the fertilized ovule, the next
generation of a particular plant species
undergoes a series of events that at times seems
impossible for a living organism. After a
period of time marked by the accumulation of
storage material, and growth of an embryo,
unknown events occur that signal the cessation
of processes related to maturation and the
ripening of the seed begins with the gradual
dehydration of all organs and tissues. Many
seeds dehydrate to a moisture content of about
10%, and the only measurable process is a much
reduced rate of oxygen uptake. Apparently,
maturing seeds have a requirement for the loss
of water below some critical level before
germination can begin. Sung et al. (1987)

---

[1]Plant Physiologist, USDA-ARS, Foreign
Disease-Weed Science Research, Fort Detrick,
Bldg. 1301, Frederick, MD 21701

reported that barnyardgrass [Echinochola
crus-galli (L) Beauv.] seeds required
dehydration to approximately 18% moisture
content before germination could be induced.
Evans et al. (1975) found that the hormonal
control system for alpha-amylase in barley
(Hordeum vulgare) aleurone layers appeared to
only operate fully after the grain had lost
moisture. This requirement to lose moisture is
related to the switching of processes from one
of storage and accumulation to one of hydration
for enzymes, cell membranes, and hydrolysis
(Dasgupta and Bewley 1982; Misra and Bewley
1985). It is from this dry, quiescent state
that the process of germination begins.

Environmental Requirements

Germination and very early seedling growth have
few environmental requirements because the seed
contains the necessary stored products to carry
out metabolic processes. Water is the first and
foremost requirement for germination and unlike
other environmental requirements, does not vary
greatly among plant species. The range of
moisture stress under which seed germination can
occur is very narrow and seldom exceeds -1.0
MPa. Although some seeds have adaptive features
such as mucilage production to attract and
retain moisture, the low water potential of the
seed is the driving force for the uptake of
water. The role of water in the germinating
seed is discussed in detail in later sections.

If the water requirement for germination is met,
temperature becomes important. Because the
speed of biochemical reactions is temperature
dependent, the time required for germination is
also temperature regulated. Temperatures above
a certain maximum and duration will be
detrimental to the seed, presumably because
enzyme activity is reduced or the proteins are
denatured. Low temperatures reduce metabolic
activities and some seeds may enter secondary
dormancy, blocking the germination process.
Species differ greatly with respect to
temperature requirements relative to maximum and
minimum ranges for optimum germination.
Generally, seeds are capable of germination
between 5 and 40 C. Leather and Sung (1983) for
example, found that native wild sunflower
(Helianthus annuus) seeds collected from Arizona
mountains germinated well at constant 5 C. A
number of species require diurnal thermo-
periodicity for germination. Apparently, there
is a critical temperature level that must be
exceeded before germination can proceed at a
lower temperature (Koller and Hadas, 1982).

Many, but not all plant species, require oxygen
for germination. Oxygen is necessary as the
terminal acceptor of electrons in respiration
and for oxidative phosphorylation in the
production of ATP. It is not understood how
seeds such as barnyardgrass that germinate
anaerobically (Kennedy et al., 1980) meet their
requirements for metabolic energy. Because of
the low solubility of oxygen in water, there are
questions regarding the need for oxygen during

imbibition (Koller and Hadas, 1982). However, reduction in the available oxygen reduces germination in many species other than those that germinate anaerobically. Possibly, germination can proceed without oxygen but further radicle growth requiring cell division and attending metabolic processes may be the first oxygen requiring event.

Imbibition

Water is the first requirement for the maturation, desiccation, and the germination of seeds. For the mature dry seed, the process of rehydration begins when water becomes available. Availability of water and uptake by the seed depend upon several factors including the relationship between the seed and its substrate and water potential of the seed cells. In soil, uptake will be influenced by the total area of seed in contact with the soil and the soil matric potential. Features of the seed coat such as impermeability or selective permeability will have an affect on water uptake (Egley and Paul 1982). In some cases permeability may be the determining factor as to the dormancy of a seed. Saha and Takahashi (1981) found that dormant Crotalaria seeds were incapable of imbibing water while nondormant seeds imbibed and germinated. Scarification of dormant seeds often leads to imbibition and subsequent germination. It is interesting that seeds which they determined to be dead imbibed water in much the same pattern as germinable seeds and to a greater extent than dormant seed.

The pattern of water uptake in seeds is triphasic (Koller and Hadas 1982). The first or initial stage is characterized by rapid saturation kinetics typical of non-biological absorption and occurs in dead as well as viable seeds. In viable seeds, there is an increase in respiration and oxidative phosphorylation and this is the time of membrane reorganization. In some seeds, imbibition in cool temperatures results in leakage of electrolytes as well as amino acids and proteins, thus indicating poorly organized cell membranes (Pollock 1969, Simon 1979, Woodstock and Tao 1981, Woodstock and Taylorson 1981, Vertucci and Leopold 1984). This initial imbibition phase is temperature dependent, but seed volume increases or total uptake of water cannot be explained by the temperature effects on the energy status or viscosity of the water (Leopold 1983).

The second, or transition phase is characterized by little increase in moisture content or respiration rate, and the morphology of the seed is generally unchanged. There are however, changes in activities of organelles such as polysomes, and this period is probably the time that major metabolic events occur in preparation for radicle protrusion. Although Spedding and Wilson (1968) observed ^{3}H-labelled amino acids in Sinapis alba seeds 5 min. after imbibing tritiated water, they had removed a portion of the seed coat which certainly enhanced the speed of imbibition. They observed also that Krebs cycle acids became labelled 30 min. after the beginning of imbibition. Similar results were obtained with bean (Phaseolus vulgaris) axes (Collins and Wilson, 1972) and barley embryos (Collins and Wilson, 1975). In the unaltered seed, the time for labelling of these metabolites would be greater and may correspond to this lag phase of water uptake. These metabolic events are probably the least understood processes of seed germination. Seeds that are in this transition phase of water uptake can be desiccated and re-imbibed without harm. Morohashi and Bewley (1980) however, found that mitochondrial activity was reduced in pea (Pisum sativum) cotyledons that were imbibed and subsequently dried. After a series of three consecutive imbibition and drying cycles, the activity was only 59% of those imbibed once. Koller and Hadas (1982) suggest that this may be the time in which seeds enter secondary dormancy if conditions do not permit initiation of the third phase.

The final phase of water uptake occurs only in viable, non-dormant seeds and is generally associated with radicle protrusion. It is accepted that radicle growth at this phase is by cellular extension and does not require utilization of stored materials. During this time, there is again a rapid increase in the water uptake associated with increased respiration and oxygen requirements.

What is the nature of water in imbibing seeds? Samuilov et al. (1976) used nuclear magnetic resonance (NMR) spin echo to investigate relaxation of water protons. They found that the state of water in the seed changed significantly during the imbibition processes and could be divided into four fractions which differed with respect to their properties and interactions with different cell components. These fractions can be closely correlated with the three phases of imbibition previously described. The first fraction identified by Samuilov et al. (1976) is that of bound water and it is maintained until a water content of 15% in the seed is attained. This bound water is water of hydration of proteins, water bound to starch, and water mechanically immobilized by structural proteins. The second fraction is water that is associated with the hydration of starch and is free water. These first two fractions were identified during the initial, rapid phase of water uptake. During the period corresponding to the transition phase of imbibition, a third fraction of water was associated with storage proteins, and the fourth fraction with structural proteins of the embryo during the final phase of water uptake.

Radicle Protrusion

The protrusion of the radicle through the seed testa is the visible indication that the germination process is complete. The physical and biochemical events which result in the final thrust of the radicle through the testa are of special interest at the present time.

Hsiao et al. (1983) using dormant wild oat
(_Avena fatua_ L.) seed, found that germination
could be induced by puncturing the testa and
that localized changes in water potential
appeared to be responsible for increased water
uptake necessary for radicle elongation. They
based their hypothesis on results that showed
differential water uptake by the embryo related
to the distance the puncture was made from the
embryonic axis. Sung et al. (1987) reported
similar response to puncturing in dormant
barnyardgrass seeds, but they suggest a wounding
response which triggers a biochemical event
associated with increased water uptake by the
radicle cells.

Schopfer and Plachy (1984, 1985) have
investigated the requirements of water uptake
and cell wall extensibility for radicle cell
elongation. From these studies and those of
others (McIntyre and Hsiao 1985), it is apparent
that radicle elongation is dependent upon a
decrease of water potential within those cells
that extend during germination. Schopfer and
Plachy (1984) presented evidence that abscisic
acid (ABA) inhibits seed germination by blocking
the osmotic mobilization of water. They later
reported (Schopfer and Plachy 1985) that
reorientation of the cell wall components was
necessary to allow extension, and that may be
the controlling point of ABA. Cell extension in
plant tissues is generally held to be regulated
by hormones, especially auxins and gibberellins
(Bewley and Black 1978). There is little
evidence that this is the case in radicle cell
elongation during germination.

From studies using dormant seeds, we may soon be
able to define those yet unknown physical and
biochemical events leading to germination that
occur rapidly and often simultaneously in
viable, non-dormant seeds and explain the
mysterious process of germination.

LITERATURE CITED

Bewley, J. D. and M. Black. 1978. Physiology
and Biochemistry of Seeds. Vol. 1.
Development, Germination and Growth.
Springer-Verlag. Heidelberg.

Bewley, J. D. and M. Black. 1982. Physiology
and Biochemistry of Seeds. Vol. 2.
Viability, Dormancy and Environmental
Control. Springer-Verlag. Heidelberg.

Collins, D. M. and A. T. Wilson. 1972.
Metabolism of the axis and cotyledons of
Phaseolus vulgaris seeds during early
germination. Phytochem. 11:1931-1935.

Collins, D. M. and A. T. Wilson. 1975. Embryo
and endosperm metabolism of barley seeds
during early germination. J. Exp. Bot.
26:737-740.

Dasgupta, J. and J. D. Bewley. 1982.
Desiccation of axes of _Phaseolus vulgaris_
during development of a switch from a
development pattern of protein synthesis to a
germination pattern. Plant Physiol.
70:1224:1227.

Egley, G. H. and R. N. Paul, Jr. 1982.
Development, structure and function of
subpalisade cells in water impermeable sida
spinosa seeds. Amer. J. Bot. 69:1402-1409.

Evans, M., N. Black and J. Chapman. 1975.
Induction of hormone sensitivity by
dehydration is one positive role for drying
in cereals. Nature 258:144-145.

Hsiao, A. I., G. I. McIntyre and J. A. Hanes.
1983. Seed dormancy in Avena fatua. I.
Induction of germination by mechanical
injury. Bot. Gaz. 144:217-222.

Kennedy, R. A., S. C. H. Barrett, D. Vander Zee
and M. E. Rumpho. 1980. Germination and
seedling growth under anaerobic conditions in
Echinochloa crus-galli (barnyardgrass).
Plant Cell Environ. 3:243-248.

Khan, A. A., Ed. 1982. The Physiology and
Biochemistry of Seed Development, Dormancy
and Germination. Elsevier Biomedical Press.
Amsterdam.

Koller, D. and A. Hadas. 1982. Water relations
in the germination of seeds. In pp 401-433.
O. L. Lange, P. S. Nobel, C. B. Osmond, and
H. Ziegler. Eds. Physiological Plant
Ecology II. Springer-Verlag. Berlin,
Heidelberg.

Leather, G. R. and S-J. S. Sung. 1983.
Ecological significance of native wild
sunflower seed germination patterns. Plant
Physiol. Supp. 72:98.

Leopold, A. C. 1983. Volumetric components of
seed imbibition. Plant Physiol. 73:677-680.

McIntyre, G. I. and A. I. Hsiao. 1985. Seed
dormancy in _Avena fatua_. II. Evidence of
embryo water content as a limiting factor.
Bot. Gaz. 146:347-352.

Misra, S. and J. D. Bewley. 1985.
Reprogramming of protein synthesis from a
developmental to a germinative mode by
induced desiccation of the axes of _Phaseolus
vulgaris_. Plant Physiol. 78:876-882.

Morohashi, Y. and J. D. Bewley. 1980.
Development of mitochondrial activities in
pea cotyledons. Plant Physiol. 66:637-640.

Murray, D. R., Ed. 1984a. Seed Physiology.
Vol. 1, Development. Academic Press.
Orlando, FL.

Murray, D. R., Ed. 1984b. Seed Physiology. Vol. 2, Germination and Reserve Mobilization. Academic Press. Orlando, FL.

Pollock, B. M. 1969. Imbibition temperature sensitivity of lima bean seeds controlled by initial seed moisture. Plant Physiol. 44:907-911.

Saha, P. K. and N. Takahashi. 1981. Seed dormancy and water uptake in *Crotalaria sericea* Retz. Ann. Bot. 47:423-425.

Samuilov, F. D., V. I. Nikiforov and E. A. Nikiforov. 1976. Use of nuclear magnetic resonance to study the state of water in germinating seeds. Soviet Plant Physiol. 23:480-484.

Schopfer, P. and C. Plachy. 1984. Control of seed germination by abscisic acid. II. Effect on embryo water uptake in *Brassica napus* L. Plant Physiol. 76:155-160.

Schopfer, P. and C. Plachy. 1985. Control of seed germination by abscisic acid. III. Effect of embryo growth potential (minimum turgor pressure) and growth coefficient (cell wall extensibility) in *Brassica napus* L. Plant Physiol 77:676-686.

Simon, E. W. 1979. Seed germination at low temperatures. *In* pp 37-47. J. M. Lyons, D. Graham and J. K. Raison, Eds. Low Temperature Stress in Crop Plants. Academic Press, New York.

Spedding, D. J. and A. T. Wilson. 1968. Studies of the early reactions in the germination of *Sinapis alba* seeds. Phytochem. 7:897-901.

Sung, S-J. S., G. R. Leather and M. G. Hale. 1987. Development and germination of barnyardgrass (*Echinochloa crus-galli*) seeds. Weed Sci. 35:211-215.

Vertucci, C. W. and A. C. Leopold. 1984. Bound water in soybean seed and its relation to respiration and imbibitional damage. Plant Physiol. 75:114-117.

Woodstock, L. W. and K-L. J. Tao. 1981. Prevention of imbibitional injury in low vigor soybean embryonic axes by osmotic control of water uptake. Physiol. Plant. 51:133-139.

Woodstock, L. W. and R. B. Taylorson. 1981. Soaking injury and its reversal with polyethylene glycol in relation to respiratory metabolism in high and low vigor soybean seeds. Physiol. Plant. 53:263-268.

SEEDLING MORPHOLOGY AND ANATOMY OF RANGELAND PLANT SPECIES

Charles R. Tischler and Paul W. Voigt[1]

ABSTRACT

Range grasses are difficult to establish because of their morphological development, coupled with the hostile environments in which they are grown. The limitations are greatest for warm season grasses. Features such as leaf wax and an anatomy conducive to leaf rolling may also modify establishment of rangeland plants.

INTRODUCTION

To thoroughly cover the topic of "Seedling Morphology and Anatomy of Rangeland Plant Species" is a major order. A realistic approach is to limit the topic to those items of general interest to the audience, emphasizing the particular morphological and anatomical features which are important in affecting establishment and which could be changed by breeding and selection, or which could be accommodated or compensated for by modifying cultural conditions. For this symposium, we limit discussion to the period of time between visible germination and seedling establishment. An established plant is one which has adequate root penetration into the soil to maintain a favorable water potential in the shoot. For grasses, the possibility adequate water supply to the shoot requires the presence of one or more nodal roots penetrating into moist soil. Drought tolerance will not be covered, although some elements of drought avoidance will be covered. Although seedling vigor, because it influences the rate at which a plant reaches a given level of morphological development, can be considered to influence morphology, it will not be considered in this discussion, because the less vigorous plant would achieve the degree of development of the more vigorous plant, given enough time.

GENERAL ROOT MORPHOLOGY OF MONOCOTS AND DICOTS

The radicle in dicots gives rise to the tap root system of the plant. This organ initiates growth at germination, and continues to elongate. The diameter of the primary root may increase with time, because it is normally capable of undergoing secondary growth. In monocots, the radicle gives rise to the seminal root system. This root system is generally short-lived, and is replaced by nodal or adventitious roots arising from the coleoptilar or higher nodes. The fact that the seminal root system in most cases is

---

[1]Plant Physiologist and Research Geneticist, respectively, USDA-ARS, Grassland Soil and Water Research Laboratory, P. O. Box 6112, Temple, Texas 76503-6112.

temporary is a primary cause for the difficulty often experienced in establishing grasses.

TYPES OF SEEDLING MORPHOLOGY OBSERVED IN MONOCOTS

A series of papers in the 1930's reviewed the classical literature concerning the below ground organs of important monocotyledons. In trying to establish order from chaos concerning types of grass seedling morphology, McCall (1934) recognized three types of development as exemplified by corn (Zea mays L.), wheat (Triticum aestivum L.), and oats (Avena sativa L.). Boyd and Avery (1936) disagreed with McCall on certain points, indicating that the developing physiological interest in Avena as a tool for studying hormone bioassay required a consistent nomenclature and delineation of structure, but both McCall and Boyd and Avery agreed that "mesocotyl" was an objectional term. As is not uncommon, the anticipated audience was (and is) among the last to learn the message. The author, being somewhat typical of physiologists, abandoned the term only several years beyond termination of formal education. The term "mesocotyl" arose because of an abandoned tenant of grass embryology which held that the scutellum and coleoptile together form the cotyledon (McCall 1934). In the words of McCall, ". . . the axis interval between scutellum and coleoptile attachments is interpreted as nodal, or "middle" of the cotyledon, hence the mesocotyl of maize. . . ." Using the terminology of Hyder et al. (1971), this structure will be referred to as the "subcoleoptile internode". It must be kept in mind that some contemporary authors still prefer to call the structure a mesocotyl.

Perhaps a more useful classification of grass seedling types was presented by Hoshikawa (1969). He documented seedling morphology of 219 grass species (88 genera) and arrived at a classification based on six types of seminal (seed derived) organs and seven types of seedling establishment.

A schematic diagram illustrating the organs recognized by Hoshikawa is presented in figure 1. Contrary to the terminology used in his paper, we use the term subcoleoptile internode rather than mesocotyl. The classifications of Hoshikawa are based on the presence or absence of "transitory node roots" (more correctly called "seminal lateral roots"), the elongation or non-elongation of the subcoleoptile internode, and the presence or absence of roots on the subcoleoptile internode. The primary root and coleoptile are, of course, always present.

The following discussion will, with certain exceptions, parallel the six types of seminal organs described by Hoshikawa. Particular emphasis will be placed on the differences between grasses in the subfamily Festucoideae, most of which do not have a discernable subcoleoptile internode, and grasses in the subfamily Panicoidae, all of which possess a

subcoleoptile internode. The morphologies characteristic of these two subfamilies are normally called "Festucoid" and "Panicoid," respectively. Admittedly, this classification is far from exact and exceptions exist. Also, some may consider it inappropriate to apply these terms to grasses not in the subfamily Festucoideae or Panicoidae. We chose, at present, to use these terms rather than to coin additional terms.
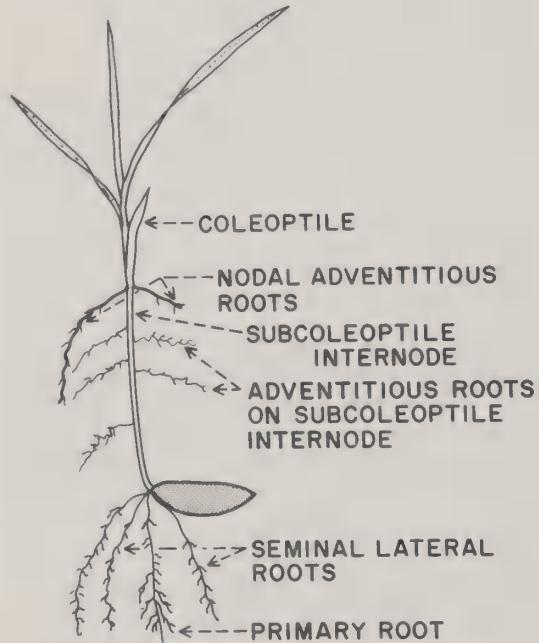
Figure 1. Morphological features of the grass seedling.

MAJOR STRUCTURES OF THE MONOCOTYLEDON SEEDLING

Root Hairs on the Coleorhiza and Epiblast

Root hairs are observed on the coleorhiza and epiblast of many germinating seed (Brown 1960). Apparently no comprehensive study of these structures in forage grasses has been made. It might be interesting to speculate that genotypic differences in establishment from surface seedings (for example, see Cox and Martin 1984) may relate to the presence or degree of development of these structures. That these structures function in anchoring the seed to the soil was well described and referenced by Haberlandt (1914) in his classical text "Physiological Plant Anatomy."

The Primary Root

The primary root, under normal conditions, is a short-lived structure which is eventually replaced by adventitious roots arising from the plant crown. On occasion the primary root may be absent, as Tischler and Voigt (1981) observed for kleingrass (Panicum coloratum L.) and weeping lovegrass (Eragrostis curvula (Schrad.) Nees). Frequency of this defect was influenced by temperature, seed mass, and the presence of

butyric acid in the germination media. Also, Tischler and Monk (1980) observed that in kleingrass, elongation of the primary root is a biphasic process. A limited amount of elongation occurs (approximately 0.6 cm), and growth stops until the coleoptile perceives light. Thus, in deep planting the seminal root grows only about 0.5 cm below the seed and grows no further until the coleoptile reaches the soil surface. The deep planted seed explores no deeper for moisture than the shallow planted seed. Its only advantage is initially better protection from surface drying and a requirement for greater precipitation to initiate germination, because more precipitation is required to wet the profile to a greater depth. This amount of precipitation will increase the probability of successful germination and seedling establishment.

The literature contains contradictions relative to the length of time that a grass seedling can subsist on the primary root. Weaver and Zink (1945) reported that blue grama (Bouteloua gracilis (H.B.K.) Lag.) seedlings in the greenhouse limited to the primary root died within 9 weeks, while van der Sluijs and Hyder (1974) reported that blue grama may actively grow for 22 weeks in the greenhouse when restricted to the primary root. We have found that primary roots of 'Ermelo' weeping lovegrass and 'Catalina' boer lovegrass (Eragrostis curvula var. conferta Nees) will penetrate to a depth of at least 50 cm in a friable soil when adventitious roots are not allowed to develop.[2] However, it must be remembered that a loose, friable soil is not the normal condition experienced on rangelands. In this regard, Wilson and Briske (1979) indicated that under favorable conditions, blue grama seedlings initiate crown roots to replace the function of the primary root as early as two weeks after planting. As will be discussed later, seedling failures with many panicoid grasses occur when dry surface soil prevents crown root development. As a result, the primary root and subcoleoptile internode cannot supply sufficient moisture to keep up with increasing evaporative demand of the growing shoot. Shoot hydration cannot be maintained (Wilson and Sarles 1978).

Both growing media and rooting volume are critical in studies of seedling root and shoot growth. O'Brien (1978) found that the culture medium can influence relative performances of cultivars in terms of root dry weight. Peterson et al. (1984) demonstrated that restricted rooting volume modifies tillering and shoot growth in wheat. In studies of root morphology and shoot growth, a soil should be employed that is representative of the soil types where the grass is actually grown. Soil conditions such as compaction or hard pan layers should be considered also. Rooting volume should be adequate for the size of the plant to be grown. Remember also that restricting seedlings to seminal roots is likely to alter shoot development and morphology.

---

[2]Tischler and Voigt, unpublished observation.

Seminal Lateral Roots

Because these roots do not arise from the primary root axis of the embryo, they must be considered to be adventitious roots (Esau 1977) although Hyder (1974) classifies adventitious and seminal roots separately. In general, seminal lateral roots are commonly observed in festucoid grasses. Hoshikawa (1969) did not observe them in panicoid grasses. A brief mention should be made of the role of these roots in cereals. A substantial body of literature has developed relative to the numbers of these roots and also their anatomy (metaxylem vessel radii) as these characteristics influence survival and seed production in arid regions. Meyer and Alston (1978) give an adequate coverage of these topics, and their importance for wheat yield. The potential for seminal lateral root production has been demonstrated to be of adaptive significance when the primary roots of crested wheatgrass (Agropyron desertorum (Fischer ex Link) Schultes) and Russian wildrye (Psathyrostachys juncea (Fischer) Nevski) were killed by drought (Hassanyar and Wilson 1978). This is a good example of the potential of a flexible plant morphology to aid in seedling establishment. Fulbright et al. (1984) observed similar behavior in green needlegrass (Stipa viridula Trin.), where seminal lateral roots developed after the primary roots of germinating seedlings were killed by drought.

The Subcoleoptile Internode

This interesting structure elevates the coleoptile to the soil surface in species that do not have the capability for significant coleoptile elongation. Boyd and Avery (1936) observed that the subcoleoptile internode does not have true stem character, but rather an intermediate anatomy which is neither exarch or endarch. Brown (1960) summarizes various arguments concerning the identity of the structure, and forcefully states, it ". . . is neither a node nor an internode but a structure peculiar to the embryo . . . it is unlike an internode since the intercalary meristem remains just below the coleoptile . . . where the intercalary meristem of an internode remains below the tissue it produces. . . ." This reversed behavior could be interpreted as a modification to aid emergence. Hyder (1971) states that the ". . . meristematic tissue located at the upper end of the subcoleoptile internode . . ." is an adaptation for pushing the coleoptile to the soil surface which is probably superior to elongation in the coleoptile itself. This type of morphology is detrimental only in regions with limited precipitation. Hyder (1971) diplomatically states that in defining panicoid and festucoid type morphology, ". . . the presence or absence of an obvious subcoleoptile internode is sufficient identification of external morphological form. . . ." The word "obvious" is important, because the cross sectional anatomy of both panicoid and festucoid seedlings is very similar, with the difference in type resulting from differential elongation of the first internode (Boyd and Avery 1936).

Adventitious roots frequently arise from the subcoleoptile internode. The value of these structures in relatively dry soil is probably questionable, as they are less likely to contribute to the water economy of the shoot than are the primary root or seminal lateral roots. However, they are possibly very important in situations where soil moisture conditions are moderate and the seedling primary root is damaged or missing.

Wilson et al. (1976) suggested that subcoleoptile internode anatomy (in terms of radius of xylem vessels) provides a major resistance to water transport from the primary seminal root to the shoot of blue grama. His paper gives an excellent treatment of the effects of this limitation on leaf area development in this species, and should be read in depth by those interested in this topic. A similarly excellent paper by Cornish et al. (1984) presents similar conclusions for ryegrass (Lolium perenne L.) and phalaris (Phalaris aquatica L.).

The Coleoptile

Historically, morphologists have held many views concerning the evolutionary origin of the coleoptile. McCall (1934) summarizes the classical arguments on this topic. Of the various interpretations given, we were most appreciative of Boyd's summary statement that "Holzner confessed his inability to arrive at any definite decision." Avery (1930) succinctly defined the coleoptile as ". . . the growing point of the stem together with embryonic leaves being enclosed within it." There can be no disagreement with the statement of Hyder et al. (1971) that ". . . the coleoptile is the structure of grasses adapted specifically for seedling emergence." In festucoid grasses, the coleoptile elongates to a lesser or greater degree to elevate the shoot structures to the soil surface. The ability of the coleoptile to elongate is limited. A vast body of literature exists relative to the agronomic significance and the genetic considerations of this limitation in wheat. For both wheat and festucoid forage grasses (having no subcoleoptile internode elongation), planting seed deeper than the elongation potential of the coleoptile results in leaves emerging from the coleoptile below the soil surface. Seedlings encountering this situation may not survive, as ". . . Foliage leaves are poorly adapted to force themselves through the soil above the reach of the coleoptile . . ." (Hyder et al. 1971).

Elongation of the coleoptile occurs as the second internode elongates. Contrary to the situation for subcoleoptile internode elongation, the second internode elongates because of cell divisions on the lower side of the internode (Brown 1960). The node giving rise to this elongation will be called the coleoptilar node, in agreement with Hyder (1971). Nodal (adventitious) roots are initiated from the coleoptilar node. Also, as Hyder indicates, emergence from relatively deep plantings may

involve cell divisions in nodes superior to the coleoptilar node.

The Coleoptile Tiller

Some festucoid grasses have the capacity to initiate a tiller in the axis of the coleoptile. Lewis and Garcia (1978) observed the development of this structure in tall fescue (Festuca arundinacea Schreb.). They found that a developed coleoptile tiller was associated with much higher seedling vigor, and they suggested selection for presence of a coleoptile tiller as a method to improve seedling vigor in the species. Coleoptile tillers may also develop in wheat. Peterson et al. (1982) report that the development of this tiller occurs most frequently in seedlings arising from large seed which subsequently received "adequate irradiance levels during seedling growth." This observation suggests that in wheat, coleoptile tiller development is not itself a morphological characteristic which confers seedling vigor, but rather more a manifestation of seedling vigor. Faulkner et al. (1982) demonstrated that two cycles of selection can greatly increase the frequency of coleoptile tillers in tall fescue, but advances in vigor that were realized by selecting for a coleoptile tiller were no greater than if selection was based on vigor per se.

Significance of the Location of the Coleoptilar Node

The difference in panicoid and festucoid morphology assumes great importance to the range scientist when grasses are seeded in arid environments. Because nodal roots arise at the coleoptilar node, the location of this node consequently dictates whether these roots arise at planting depth or essentially at the soil surface (figure 2). These considerations have been excellently described in the literature, but brief examples will be presented for the benefit of those not familiar with the topic. For the festucoid grass, nodal roots are initiated at planting depth in the soil profile. For the panicoid grass, adventitious roots are initiated at less than 0.5 cm in the soil profile. Obviously, the coleoptilar node at the shallow depth would be much more likely to be in dry soil than the coleoptilar node at 3 cm. Hyder et al. (1971) attributed blue grama (panicoid) seedling failures to this morphology while crested wheatgrass (Agropyron desetorum (Fisch. ex Link) Schult.) (festucoid) seedlings become successfully established in adjacent plots. As previously indicated, the primary seminal root (and in panicoid grasses, the subcoleoptile internode) have a limited potential for water transport to the shoot. Cornish et al. (1984) calculated that for ryegass and phalaris, conductance of each nodal root axis is more than 100 times greater than the conductance of the primary seminal root (even ignoring the resistance of the subcoleoptile internode).
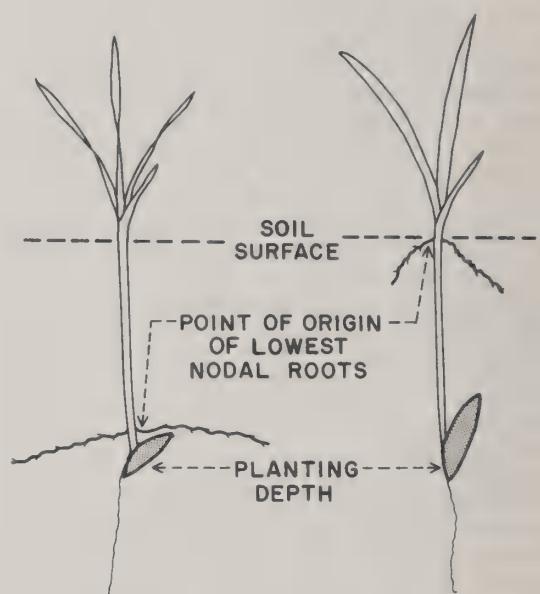
Figure 2. Point of origin of nodal roots in festucoid and panicoid grasses.

The potential advantages of festucoid morphology are realized only in very specific situations. First of all, if soil moisture is adequate and temperatures are in reasonable ranges, grass seedlings of either morphology should become established with equal success. Secondly, from very shallow planting depths (0.5 cm or less), the festucoid morphology confers no advantage, as the subcoleoptile internode of panicoid grasses undergoes minimal elongation. Also, from excessively deep planting depths, panicoid grasses are more likely to emerge than festucoid grasses, because the subcoleoptile internode appears to have the potential for greater elongation than does the coleoptile. However, within given environmental constraints, the advantages of festucoid morphology are unquestionable. The morphological limitations of panicoid grasses are aggravated by a physiological limitation. Panicoid grasses are generally C4 warm season grasses, and of lesser cold tolerance than C3 festucoid grasses. Thus, in many cases, panicoid grasses normally cannot be planted in the fall and still reach an adequate size to overwinter. This limitation dictates that panicoid grasses be planted in the spring, when cold weather has passed, so that the panicoid seedlings potentially face the likely prospect of summer drought. On the other hand, festucoid grasses can grow more effectively in early spring or fall when evaporative demand is less because of lower temperature. Therefore, even if adventitious roots were being initiated from the same level in the soil, festucoid grasses would have an advantage because the top 2 cm of the will not dry as quickly at cooler temperatures. A good treatment of the interaction of moisture and temperature in regulating adventitious root initiation and

growth in blue grama is given by Briske and Wilson (1978). Also, the reader is referred to Wilson et al. (1976), and the references cited therein, for an excellent coverage of the entire topic.

Other work from Wilson's laboratory (Fulbright et al. 1985) describes the seedling morphology of green needlegrass (Stipa viridula Trin.), a grass with limited subcoleoptile internode elongation. The maximum extent of subcoleoptile internode elongation observed for two strains was 1.4 and 1.1 cm from planting depths of 6.0 cm. Consideration of soil type is also necessary in selecting a planting depth, as this species in general exhibits poor emergence from clay soils.

An inspection of field plantings of panicoid grasses often reveals that in many seedlings, the coleoptile base (coleoptilar node) is a short distance above the soil surface, with the seedling "hanging on" to the soil by the subcoleoptile internode. Olmstead (1941) commented on this phenomena in sideoats grama (Bouteloua curtipendula), stating that ". . . seventy-two hours after initial watering, tips of coleoptiles were emergent 5-10 mm above the soil surface. Twenty-four hours later, elongation of the first internode (mesocotyl) had ceased, bringing the coleoptile node to the ground line, or in a few cases as much as 8 mm above it. These latter plants, in the . . . (drier) . . . treatments rarely succeeded in establishing adventitious roots. . . ." To explain why the coleoptile base is observed to be above the soil surface requires a brief consideration of the control of elongation of the subcoleoptile internode and/or coleoptile. Contrary to the author's expectations, very little is known about the mechanisms by which light regulates (slows or stops) elongation of these organs. Apparently no work has been done on this topic using forage grasses. The work I will cite was performed using cereal crops, but the physiological mechanisms involved should be similar.

Because of the great interest in the etiolated Avena coleoptile as a bioassay tissue for auxin, Johnson (1937) determined the specific wavelengths responsible for the cessation of elongation of the first internode were in the red region of the spectrum. The same conclusion was drawn by Weintraub et al. (1947). Vanderhoef and Briggs (1978) undertook a more detailed study of the physiology of the response in corn and validated the hypothesis of van Overbeek (1936), that light regulates elongation of the first internode by controlling auxin supply from the coleoptile. In a second series of experiments with corn, Vanderhoef et al. (1979) explored the sensitivity of this response to red light. Two separate responses appeared to be involved, which required different amounts of red illumination. Recent evidence suggests that control of first internode elongation may be even more complex. Parks and Poff (1986) present evidence that the tip of the coleoptile is not the perceptive site, but rather that light travels down the coleoptile to a site below the coleoptilar node, where the signal is perceived. To accommodate the

observations of Vanderhoef and Briggs (1978), Parks and Poff (1986) hypothesize that the receptive site below the coleoptilar node, once it perceives light transmitted down from the coleoptile tip ". . . affects coleoptilar auxin supply through some unknown mechanism. . . ."

The significance of these observations for the range scientist deal with the location of the coleoptilar node relative to the soil surface. Extrapolating from the data of Vanderhoef et al. (1979), from the time the corn coleoptile perceives continuous red light, the subcoleoptile internode elongates approximately 8 mm. The elongation rate of the subcoleoptile internode in darkness is about 2.4 mm per hour. If we accept a coleoptile length in corn of approximately 3 cm, then if a coleoptile tip broke the soil surface and immediately experienced saturating red light, elongation would cease when the coleoptilar node was 2.2 cm below the soil surface. If, however, the coleoptile tip broke the soil surface at sundown, elongation would continue at the 2.4 mm per hour rate (assuming constant temperature) for approximately 11 hours, placing the coleoptilar node 0.4 cm below the soil surface at sunup. When we consider that from the initiation of light exposure, the first internode will still elongate 8 mm, the final result will be that the coleoptilar node will be located 0.4 cm above the soil surface. The appropriate figures for panicoid range grasses would probably be somewhat different. However, in the case of range grasses, we must remember that the range microenvironment can only serve to limit the duration and/or intensity of irradiation of the coleoptile. Also, cloud cover and other atmospheric conditions could keep the level of incident radiation below saturating levels. The data of Woolley and Stoller (1978) indicate that less than 1% of incident light penetrates to a depth of 2.2 mm in the soil, which suggests that the coleoptile must be essentially at the soil surface before any potental effects of light on subcoleoptile internode elongation may be realized. In summary, for grass seedlings that initiate emergence at the end of the day, it is very easy to see how they could have a coleoptilar node above the soil by the time all elongation ceases.

Nodal Roots

Roots arising at the coleoptilar or higher nodes give rise to the root system of the mature plant. As previously indicated, the potential for water conduction of a nodal root is orders of magnitude higher than that for the seminal primary root. A good treatment of the older literature on penetration, morphology, etc., of nodal roots is given by Troughton (1957). Concerning the origin of nodal roots, Bell and Parry (1976) have indicated that for Italian ryegrass, morphological and anatomical development varies between seedlings which appear visually identical. In a subsequent paper, Bell (1976) presents a comparison of coleoptilar node anatomy of a number of seedlings. He observed great differences in anatomy between different seedlings, and suggested that these differences

could affect the site or rate of development of nodal roots. Nodal root development and morphology may be influenced by environment. As previously mentioned, environmental conditions affect adventitious root initiation and elongation in blue grama. Also, root morphology may be markedly affected by environment. As an example, Perata (1935) indicated that for sudangrass (Sorghum sudanensis), increasing planting density (and consequently increasing competition) significantly reduced overall root diameter, stele diameter, and other root properties.

Although nodal root formation is of great importance for most perennial forage grasses, some perennials appear to be able to survive well on the primary root system. Watt (1981) suggested that grasses which have a well developed primary root system and a lower ratio of top growth to root growth can survive periods of drought on cracking black clay soils, and still establish (with nodal roots) when rainfall occurs. Watt presents data demonstrating that native grasses of New South Wales establish much better than introduced summer grasses for those reasons. However, the native grasses were poor forage types. We must consider the possibility that selection for a well developed primary root system and a low shoot/root ratio may not be compatable with our notion of what constitutes a desirable forage grass. These points deserve further study. Selection has been historically directed to maximize top growth, which may have only intensified problems with establishment.

Emergence Methods of Legumes

Two patterns of emergence are observed in legumes. "Hypogeous" legumes experience little hypocotyl elongation (the coleoptile remains below the soil, at planting depth), while "Epigeous" legumes experience much hypocotyl elongation (cotyledons normally are raised above the soil surface). Silcock (1980) gives a description of the variation within these plant types, and cites pertinent literature relative to the advantages of each type. Epigeous seedlings are normally considered to be at a disadvantage because ". . . the growing points of the seedling are exposed to defoliating agencies immediately after emergence and the plant can be eliminated by a single cut below the cotyledons. . . ." Hypogeous seedlings have lateral buds in the axils of the (underground) cotyledons, and can survive being cut off at ground level.

Shoot Characteristics Which May Aid in Establishment

A large number of papers have addressed the possible benefit of leaf epicuticular wax as a barrier to restrict leaf cuticular transpiration. Of course, this mechanism of water conservation becomes important only at levels of plant water stress sufficient to completely close stomates. Using a model system approach, Grncarevic and Rudler (1967) clearly demonstrated that composition rather than total amount of wax was the most important factor influencing cuticular transpiration. Jeffree et al. (1975) compared epicuticular wax structure on leaves with the subsequent structure of extracted wax that had been recrystallized, and found the two structures to be very similar. This lead them to hypothesize that composition to a large degree determines structure. Several studies have demonstrated that removal of leaf epicuticular wax modifies cuticular resistance. As an example, O'Toole et al. (1979) observed tht removal of wax decreased cuticular resistance of rice (Oryza sativa L.) by as much as 60 percent. Wright and Dobrenz (1973) obtained preliminary evidence to indicate that high wax content was associated with seedling drought tolerance in "lehmann" lovegrass (Eragrostis lehmanniana Nees.). A subsequent paper (Hull et al. 1978) dealing with the same species demonstrated that epicuticular wax morphology was relatively consistent among drought tolerant lines, and epicuticular wax morphology itself could be used as a selection criterion. Many reports indicate that amounts of epicuticular wax are influenced by climate. Rao and Reddy (1979) measured wax contents on leaves of 17 woody species, and found ". . . The amount of wax inherently formed on leaves was directly related to ambient temperatures and light intensity and inversely correlated with precipitation and humidity. . . ." Bengston et al. (1978) demonstrated that wax levels in oat increase in response to stress, and that different genotypes respond to differing extents. A somewhat alarming result was that a genotype which had the highest cuticular transpiration rate when unstressed showed the most dramatic increase in epicuticular wax content and the most strongly reduced cuticular transpiration rate when grown under water stress. This observation suggests that using epicuticular wax content as a selection criterion for stress resistance will require an experimental protocol which allows full expression of genetic potential for this characteristic. Also, environmental conditions may reduce levels of wax, as Baker and Hunt (1986) report that simulated rain removes significant amounts of epicuticular wax from leaves of several species.

Leaf Rolling or Movements

Leaves of many grasses possess bulliform cells which aparently function in leaf rolling (Esau 1977), although Shields (1951) found that rolling can also occur in leaves not having bulliform cells. O'Toole and Cruz (1979) verified that rolling does reduce transpiration in rice, while Renard and Demessemacker (1983) made similar observations for tall fescue (Festuca arundinacea Schreb.). In a thorough study of leaves of 39 grass species from Western Canada, Redmann (1985) found that ". . . all species from dry habitats had narrow or rolled leaves. . . ." These reports indicate the obvious advantages of an anatomy conducive to leaf rolling as a water-conserving mechanism for rangeland grasses.

Analogous to leaf rolling in monocots, dicotyledonous plants appear to possess a morphological characteristic aiding in stress

avoidance. Ludlow and Bjorkman (1984) report that Siratro (<u>Macroptilium atropurpureum</u>) leaves are capable of paraheliotropic leaf movements which serve to minimize radiation interception, and thus (under water stress) avoid heat damage or chlorophyll photooxidation. Meyer and Walker (1981) observed similar movements in soybeans (<u>Glycine max</u> (L.) Merr.). Perhaps this type of behavior also exists in rangeland legumes. Begg (1980) presents a fairly recent review of this topic.

SUMMARY

Grasses are more difficult to establish than dicots because the primary root system of the grass plant is short lived and must be replaced by nodal adventitious roots. In contrast, the radicle of the dicot elongates and remains functional throughout the life of the plant. Two types of morphology are recognized in grasses. Species where elongation of the first internode is observed are termed "panicoid;" those where no first internode elongation is observed are termed "festucoid". In arid regions panicoid grasses are difficult to establish because nodal adventitious roots are initiated at or near the soil surface, while the corresponding roots are initiated at or near planting depth in festucoid species. Research is needed to determine the feasibility of altering developmental processes such as subcoleoptile internode elongation, development of coleoptile tillers, etc. Anatomical and morphological features of the shoot of range plants are also important in establishment in arid regions.

LITERATURE CITED

Avery, George S. Jr. 1930. Comparative anatomy and morphology of embryos and seedlings of maize, oats, and wheat. Bot. Gaz. 89:1-39,

Baker, E. A., and Grace M. Hunt. 1986. Erosion of waxes from leaf surfaces by simulated rain. New Phytol. 102:161-173.

Begg, J. E. 1980. Morphological adaptations of leaves to water stress. <u>In</u> Adaptation of Plants to Water and High Temperature Stress, pp. 33-42. Turner, M. C., and Kramer, P. J. (eds.) Willey-Interscience, New York.

Bell, A. D. 1976. The vascular pattern of Italian ryegrass (<u>Lolium multiflorum</u> Lam.). 3. The pheripheral plexus, and nodal root insertion. Ann. Bot. 40:251-259.

Bell, A. D., and D. Wynn Parry. 1976. The vascular pattern of Italian ryegrass (<u>Lolium multiflorum</u> Lam.). 1. The young seedling and its variability. Ann. Bot. 40:223-232.

Bengtson, Curt, Stig Larsson and Conny Liljenberg. 1978. Effects of water stress on cuticular transpiration rate and amount and composition of epicuticular wax in seedlings of six oat varieties. Physiol. Plant. 44:319-324

Boyd, Lucy, and George S. Avery, Jr. 1936. Grass seedling anatomy: The first internode of <u>Avena</u> and <u>Triticum</u>. Bot. Gaz. 97:765-779.

Briske, D. D., and A. M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. J. Range Manage. 31:174-178.

Brown, W. V. 1960. The morphology of the grass embryo. Phytomorphology 15:274-284.

Cornish, P. S., J. R. McWilliam and H. B. So. 1984. Root morphology, water uptake, growth, and survival of seedlings of ryegrass and phalaris. Aust. J. Agric. Res. 35:479-492.

Cox, Jerry R., and Martha H. Martin. 1984. Effects of planting depth and soil texture on the emergence of four lovegrasses. J. Range Manage. 37:204-205.

Esau, Katherine. 1977. Anatomy of Seed Plants. 2nd edit. New York, John Wiley and Sons, 550 pp.

Faulkner, J. S., Fiona Johnston and D. M. P. McAneney. 1982. Selection for seedling vigor in <u>Festuca arundinacea</u>. J. Agric. Sci. Camb. 99:173-184.

Fulbright, Timothy E., A. M. Wilson and E. F. Redente. 1984. Effects of temporary dehydration on growth of green needlegrass (<u>Stipa viridula</u> Trin.) seedlings. J. Range Manage. 37:462-464.

Fulbright, Timothy E., A. M. Wilson and Edward F. Redente. 1985. Green needlegrass seedling morphology in relation to planting depth. J. Range Manage. 38:266-269.

Grncarevic, M., and F. Radler. 1967. The effect of wax components on cuticular transpiration--model experiments. Planta 75:23-27.

Haberlandt, G. 1914. Physiological Plant Anatomy. London, MacMillan & Co., 778 pp. (Trans. from German 4th ed. by Montagu Drummond).

Hassanyar, Amir S., and A. M. Wilson. 1978. Drought tolerance of seminal lateral root apices in crested wheatgrass and Russian wildrye. J. Range Manage. 31:254-258.

Hoshikawa, Kiyochika. 1969. Underground organs of the seedlings and the systematics of Gramineae. Bot. Gaz. 130:192-203.

Hull, Herbert M., L. Neal Wright and Charles A. Bleckmann. 1978. Epicuticular wax ultrastructure among lines of *Eragrostis lehmanniana* Nees. developed for seedling drought tolerance. Crop Sci. 18:699-704.

Hyder, D. N. 1974. Morphogenesis and management of perennial grasses in the United States. *In* Proceedings of U.S./Australian Range Science Workshop, Berkeley, Calif. U.S. Dept. Agric. Misc. Pub. 1271.

Hyder, D. N., A. C. Everson and R. E. Bement. 1971. Seedling morphology and seeding failures with blue grama. J. Range Manage. 24:287-292.

Jeffree, C. E., E. A. Baker and P. J. Holloway. 1975. Ultrastructure and recrystallization of plant epicuticular waxes. New Phytol. 75:539-549.

Johnson, E. S. 1937. Growth of *Avena* coleoptile and first internode in different wavelength bands of the spectrum. Smithson. Misc. Coll.96:1-9.

Lewis, E. J., and J. A. Garcia. 1978. The effect of seed weight and coleoptile tiller development on seedling vigor in tall fescue, *Festuca arundinacea* Schreb. Euphytica 23:393-402.

Ludlow, Mervyn M., and Olle Bjorkman. 1984. Paraheliotropic leaf movement in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. Planta 161:505-518.

McCall, M. A. 1934. Developmental anatomy and homologies in wheat. J. Agric. Res. 48:283-321.

Meyer, Wayne S., and A. M. Alston. 1978. Wheat responses to seminal root geometry and subsoil water. Agron. J. 70:981-986.

Meyer, Wayne S., and Sue Walker. 1981. Leaflet orientation in water stressed soybeans. Agron. J. 73:1070-1074.

O'Brien, L. 1978. Effect of root media on growth of wheat seminal roots. Crop Sci. 18:685-687.

Olmsted, C. E. 1941. Growth and development in range grasses. I. Early development of *Bouteloua curtipendula* in relation to water supply. Bot. Gaz. 102:499-519.

O'Toole, J. C., R. T. Cruz and J. N. Seiber. 1979. Epicuticular wax and cuticular resistance in rice. Physiol. Plant. 47:239-244.

O'Toole, J. C., and R. T. Cruz. 1979. Leaf rolling and transpiration. Plant Sci. Letters 16:111-114.

Parks, Brian M., and Kenneth L. Poff. 1986. Altering the axial light gradient affects photomorphogenesis in emergeing seedlings of *Zea mays* L. Plant Physiol. 81:75-80.

Perata, F. de. 1935. Some principles of competition as illustrated by Sudan grass, *Holcus Sorghum sudanensis* (Piper.). Hitch. Ecol. Monogr. 5:355-404.

Peterson, Curt M., Betty Klepper, F. V. Pumphroy and Ron W. Rickman. 1984. Restricted rooting decreases tillering and growth of winter wheat. Agron J. 76:861-863.

Peterson, Curt M., Betty Klepper and R. W. Rickman. 1982. Tiller development at the coleoptilar node in winter wheat. Agron. J. 74:781-784.

Rao, J. V. S., and K. Raja Reddy. 1979. Seasonal variation in leaf epicuticular wax of some semiarid shrubs. Indian J. Expt. Bot. 18:495-499.

Redmann, R. E. 1985. Adaptation of grasses to water stress--leaf rolling and stomate distribution. Ann. Missouri Bot. Gard. 72:833-842.

Renard, C., and W. Demessemacker. 1983. Effects of wind velocity on stomatal conductance and consequences of leaf rolling on water uptake in tall fescue. Biologia Plant. (Praha) 25:408-411.

Shields, L. M. 1951. The involution mechanisms in leaves of certain xeric grasses. Phytomorphology 1:225-241.

Silcock, R. G. 1980. Seedling characteristics of tropical pasture species and their implications for ease of establishment. Trop. Grasslands 14:174-180.

Tischler, Charles R., and R. L. Monk. 1980. Variability in root systems of kleingrass seedlings. Crop Sci. 20:384-386.

Tischler, C. R., and P. W. Voigt. 1981. Nongenetic factors affecting primary root absence in lovegrass and kleingrass. Crop Sci. 21:427-430.

Troughton, Arthur. 1957. The underground organs of herbage grasses. Bulletin #44. Commonwealth Bureau of Pastures and Field Crops, Hurley, Berkshire.

Vanderhoef, Larry N., Peter H. Quail and Winslow R. Briggs. 1979. Red light-induced mesocotyl elongation in maize seedlings. II. Kinetic and spectral studies. Plant Physiol. 63:1062-1067.

Vanderhoef, Larry N., and Winslow Briggs. 1978. Red light-inhibited mesocotyl elongation in maize seedlings. I. The auxin hypothesis. Plant Physiol. 61:534-537.

van der Sluijs, D. H., and D. N. Hyder. 1974. Growth and longevity of blue grama seedlings restricted to seminal roots. J. Range Manage. 27:117-119.

van Overbeek, J. 1936. Growth hormone and mesocotyl growth. Rec. Trav. Bot. Neerl. 33:333-340.

Watt, L. A. 1981. Establishment of grasses on cracking clay soils: Seedling morphology characteristics. In J. Allan Smith and Virgil W. Hays (eds.) Proc. XIV Int. Grassl. Congr. Westview Press, Boulder, CO.

Weaver, J. E., and E. Zink. 1945. Extent and longevity of the seminal roots of certain grasses. Plant Physiol. 20:359-379.

Weintraub, R. L., and L. Price. 1947. Developmental physiology of the grass seedling. II. Inhibition of mesocotyl elongation in various grasses by red and violet light. Smithson. Misc. Coll. 106 No. 21.

Wilson, A. M., and D. D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. J. Range Manage. 32:209-213.

Wilson, A. M., D. N. Hyder and K. D. Briske. 1976. Drought resistance characteristics of blue gramma seedlings. Agron. J. 68:479-484.

Wilson, A. M., and J. A. Sarles. 1978. Quantification of growth drought tolerance and avoidance of blue grama seedlings. Agron. J. 70:231-237.

Woolley, Joseph T., and Edward W. Stoller. 1978. Light penetration and light-induced seed germination in soil. Plant Physiol. 61:597-600.

Wright, L. Neal, and A. K. Dobrenz. 1973. Efficiency of water use and associated characteristics of Lehmann lovegrass. J. Range Mange. 26:210-212.

MECHANISMS OF PHYSIOLOGICAL SEED DORMANCY

Marc Alan Cohn[1]

ABSTRACT

While light, temperature, hormones, and
nonhormonal chemicals can break physiological
dormancy, mechanisms of action are not known.
However, conceptual progress has been achieved:
(1) calcium mediates light-stimulated germination;
(2) genetic studies substantiate the inhibitory
role of abscisic acid; (3) the pentose shunt
is not a controlling factor; (4) a role of
membrane structure and function is suggested by
the dormancy-breaking responses to fusicoccin,
"anesthetic"-type compounds, and weak acids.

INTRODUCTION

Seed dormancy is a state of suspended animation
which permits the survival of numerous higher
plant species under sub-optimal conditions. While
seed dormancy is advantageous to the survival of
wild species, it presents serious problems for
seed scientists and producers. In most cases,
agricultural needs are best served if dormancy is
broken prior to evaluation of seed performance,
planting, or for the efficient control of weeds.

Physiological dormancy encompasses seed dormancy
not attributable to seed coat impermeability to
water, physical restraint, or an immature embryo.
While this classification may be too rigid, it
does serve to focus upon events at the biochemical
rather than the structural level. Other systems of
classification have been proposed over the years.

There is little understanding of the mechanism by
which dormancy is terminated although many
stimuli, i.e., low temperatures, alternating
temperatures, light, dry-afterripening, plant
hormones, and a variety of other compounds have
all been identified as dormancy-breaking agents
(Bewley and Black 1982). Various hypotheses have
been proposed to account for the action of these
agents. These include inhibitor-promotor balance
(Amen 1968), activation of the pentose phosphate
pathway (Roberts and Smith 1977), stimulation of
alternative respiration (Esashi et al. 1979a,
1981a, 1981b; Yu et al. 1979), and perturbation of
membranes (Taylorson and Hendricks 1980/81).
In this review, experimental progress regarding
these hypotheses will be addressed, and additional
ideas will be presented for consideration and,
hopefully, further laboratory investigation.

THE PENTOSE SHUNT AND RELATED HYPOTHESES

The regulatory role of the pentose shunt in the
dormancy-breaking process was first elegantly
hypothesized in 1969 and developed further in
subsequent reviews (Roberts 1969, 1973; Roberts
and Smith 1977). In the pentose shunt glucose-6-
phosphate is converted to ribulose-5-phosphate via
6-phosphogluconate. At each step NADP is reduced
to NADPH. Roberts proposed that carbon flow
through the shunt was restricted in dormant seeds
because this pyridine nucleotide co-factor was
only present in the reduced form. Dormancy
breaking compounds such as nitrite, azide,
cyanide, and hydroxylamine were thought to trigger
germination by short-circuiting normal respiratory
processes and thus favoring the oxidation of NADPH
to NADP and increased pentose shunt activity. If
this hypothesis is correct, one should observe the
following events after a dormancy-breaking
treatment is imposed and prior to visible radicle
protrusion: (1) increased carbon flow through the
pentose shunt; (2) increased activity of the
regulatory enzymes of the shunt, i.e. glucose-6-
phosphate dehydrogenase and 6-phosphogluconate
dehydrogenase; (3) increased levels of NADP and
increased NADP/NADPH ratios.

Carbon flow through the pentose shunt has been
traditionally measured utilizing the ratio of 14-C
carbon dioxide released from seeds incubated with
C-1 labelled glucose and separate incubations with
C-6 labelled glucose. Results were expressed as
C6/C1 ratios. The lower this ratio, the greater
the participation of the pentose shunt compared to
the glycolytic pathway. Non-dormant and dormant
seeds treated with some, but not all, germination
triggering treatments showed C6/C1 ratios lower
than controls (Roberts 1969; Simmonds and Simpson
1971, 1972; Lacroix and Jaswal 1967, 1973).
However, increased carbon flow through the shunt
has not been confirmed in recent experiments
(Satoh and Esashi 1980; Jones and Hall 1981;
Fuerst et al. 1983). Ap Rees (1980) has presented
considerable data indicating that the C6/C1 ratio
alone is of little value in quantitating the flow
of carbon through glycolysis and the pentose
shunt.

Increased activity of the regulatory enzymes of
the pentose shunt was reported during dormancy
loss by Kovacs and Simpson (1976), but such
differences in activity seem to occur only as
postgerminative (after radicle protrusion) events
(Olusuyi 1973; Upadyhyaya et al. 1981). Low
imbibition temperatures appear to activate these
dehydrogenases independent of dormancy status
(Adkins and Ross 1981). NADP/NADPH and NAD/NADH
levels and ratios did not change with imbibition
time in dormant vs. non-dormant seeds, nor did
they change when KCN, gibberellin, or nitrite were
applied as triggering agents to dormant seeds
(Olusuyi 1973).

Based upon in vitro catalase inhibition by various
nonhormonal, dormancy-breaking chemicals,
Hendricks and Taylorson (1974, 1975) proposed that
hydrogen peroxide would facilitate oxidation of
NADPH to NADP. However, inhibition of catalase

from seeds treated with chemicals such as nitrite, azide, and hydroxylamine was not consistently associated with dormancy-breaking activity. No correlation between dormancy-breaking activity and catalase has been reported by others (Esashi et al. 1979c; Kuo 1981; Kuo and Chu 1983). The actual levels of hydrogen peroxide accumulating in the seed tissues during these treatments was not reported in any of these studies.

Therefore, while the case built for the pentose shunt hypothesis was an elegant formulation, the passage of time has exposed the weaknesses of the assumptions used to construct the hypothesis. Furthermore, experiments designed to confirm the role of the pentose shunt have not supported the predictions of the hypothesis.

A theme running thoughout Roberts' reviews concerns the contribution of an unspecified alternate pathway of respiration. Since the presentation of his initial hypothesis, the CN-resistant, hydroxamic acid sensitive pathway has been reported in many plant tissues. In a series of investigations of primary and secondary dormancy of cocklebur (Xanthium pennsylvanicum Wallr.) (Esashi et al. 1979a, 1979b, 1981a, 1981b, 1982a, 1982b), a balance between cyanide-resistant and -sensitive respiration appeared to be necessary for the termination of dormancy. There are several cautions which are relevant to these studies. 1) Seed viabilities after ineffective treatments were not reported. Therefore, it is difficult to decide whether respiratory inhibitors were inactive or killed the seeds. 2) The participation of the alternate pathway was invoked from oxygen uptake measurements performed on whole seeds. Therefore, the cyanide resistant component could not be conclusively localized in the mitochondria, nor could the contribution of other oxidases such as lipoxygenase or a plasmalemma associated redox chain be ruled out. A number of more recent investigations illustrate further weaknesses in the correlation between the alternate pathway and the dormancy-breaking process (Upadhyaya et al. 1982, 1983; Adkins et al. 1984a, 1984b, 1984c; Perino et al. 1984; Bogatek and Rychter 1984; Brooks et al. 1985). The essence of these studies suggests that both respiratory pathways are operational during the dormancy-breaking and germination processes, but that the alternate pathway is not an obligate requirement.

Cyanide has also been proposed to activate dormant seeds by acting as a carbon source for asparagine and aspartate synthesis via beta-cyanoalanine (Taylorson and Hendricks 1973). Beta-cyanoalanine could also break dormancy in Amaranthus albus L. Similar observations were reported for apple (Dziewanowska and Lewak 1982a, 1982b). However, it is not clear whether these biochemical events are unique to dormant seeds as no studies of cyanide metabolism in non-dormant seeds was reported.

Peiser et al. (1984) have demonstrated that cyanide is a natural byproduct of ethylene synthesis. Since ethylene synthesis in many instances is autocatalytic, one can speculate that cyanide has a physiologically relevant role in

species where ethylene breaks dormancy. This interesting development has yet to be evaluated for its relevance to germination.

HORMONAL REGULATION

Application of gibberellins (GA), cytokinins (CK), and ethylene, singly or in combination, will break the dormancy of many seeds, and abscisic acid (ABA) will inhibit germination. While hormones can influence metabolism at the transcriptional, translational, and membrane levels, their specific biochemical role in the dormancy-breaking process is still not clear (Khan and Samimy 1982). Furthermore, in most cases the applied concentration of hormones is in the millimolar range, which is exceedingly high. Work by Stillwell and Hester (1983, 1984), Wood and Paleg (1972), and Metzger (1983), using a variety of approaches and model systems, suggests that high levels of these growth regulators can act in a nonphysiological fashion. Extreme caution should be exercised in this regard.

Under the assumption that response to exogenous hormones was a reflection of actual events, the well-known concept of inhibitor-promoter balance was developed (Amen 1968). Dormancy would be terminated when promotors (e.g. GA, CK, ethylene) predominated while dormancy would be maintained in their absence or in the presence of inhibitors (e.g. ABA). However, studies conducted to obtain expected correlations between hormone levels and dormancy were not entirely successful for at least two reasons. 1) The techniques required to evaluate hormone concentrations were not sufficiently developed (e.g. inadequate separation techniques, unmeasured yield losses during extraction, and quantitation by bioassay) to address the question at hand. 2) The importance of tissue and cell compartmentation as well as tissue sensitivity was not recognized until recently. For example, chilling temperatures induce hormonal sensitivity in genetically GA-insensitve aleurone layers (Singh and Paleg 1984a, 1984b). ABA sensitivity changes in nondormant seeds (Finkelstein et al. 1985) and will either inhibit or promote embryogenic events depending upon the stage of seed development (Ackerson 1984). In Arabidopsis thaliana (L.) Heynh., genetic mutants containing normal or elevated ABA levels were not dormant and were 5 to 20 times less sensitive to exogenously applied ABA compared to the wild type (Koornneef et al. 1984). The importance of tissue compartmentation is also illustrated in Arabidopsis where the onset of dormancy correlated with embryonic ABA but not maternal tissue ABA. In reciprocal crosses of genetically ABA-deficient mutants and wild type of this species, dormancy developed in both the absence and presence of maternal ABA if the embryonic ABA pool was present (Karssen et al. 1983). Even proper analysis of tissue ABA may not give an accurate picture of its role in seed dormancy if inhibitor action is site specific within the cell as suggested for ABA control of stomatal aperture at the guard cell plasmalemma (Behl and Hartung 1986 and references

therein). While the inhibitor-promoter balance hypothesis has not been experimentally eliminated as a working concept and should not be abandoned, the level of sophistication at which it needs to be re-explored has increased substantially.

A ROLE FOR MEMBRANE STRUCTURE AND FUNCTION?

Dormancy can be broken by ethanol and a variety of other substances which have anesthetic properties in animal systems (Taylorson and Hendricks 1980/81; Adkins et al. 1984b; Cohn et al. 1987). These responses can be reversed by 1 MPa (10 atm) pressure during chemical treatment suggesting modification of membrane structure analogous to the anesthetic action (Hendricks and Taylorson 1980). However, seed viability of pressure-treated seeds and the effects of pressure on chemical uptake were not reported. Seeds killed by alcohol can be visually identical to dormant seeds and have a healthy appearance (Cohn et al. 1987). There is no additional evidence to suggest that membrane modification is involved in the dormancy breaking action of these compounds, nor has the possibility that such compounds act as "in vivo extractants" of germination inhibitors been satisfactorily addressed.

Fusicoccin (FC), a fungal metabolite known for its ability to stimulate proton efflux and potassium influx via plasmalemma ATPase activation in plant tissue, can either break dormancy or stimulate the germination process (Marre 1979; Foley 1986). While H+/K+ exchange is observed in seeds treated with FC, and KCl alone can stimulate RNA and protein synthesis in thermodormant Phacelia tanacetifolia Benth. seeds (Cocucci et al. 1986), the relationship between this ion exchange and initiation of biochemical activities resulting in germination remains to be identified. Foley (1986) has determined that GA, while breaking dormancy in Avena fatua L., does not stimulate ion exchange in a similar fashion. Either GA breaks dormancy through a different mechanism, or FC stimulation of H+/K+ exchange is unrelated to its dormancy breaking action. In other studies, experimental conditions which would initially favor proton influx also break seed dormancy (Palevitch and Thomas 1976; Cohn et al. 1983, 1986; Cohn and Castle 1984; Adkins et al. 1985; Cohn and Hughes 1986). A role for ion fluxes has also been suggested by the inhibition of GA stimulated germination of thermodormant celery (Apium graveolens L.) with K+ and Ca+ ionophores (Thomas and Sambrooks 1985). Presently, there is no experimental evidence to clarify this state of affairs in seeds. However, there is ample precedent for pH-mediated developmental regulation in other organisms (Busa 1986; Moolenaar 1986) as well as in the control of elongation in stems and roots (Evans 1985).

LIGHT-CONTROLLED GERMINATION: PHYTOCHROME AND CALCIUM IONS

Phytochrome is a pigment-protein complex associated with a wide spectrum of light-mediated processes in plants. Seed dormancy in many species is controlled by the ratio of the interconvertible red light and far-red light absorbing forms of this molecule. However, in seeds as well as in other systems, our knowledge of how light absorption is translated into developmental change is extraordinarily deficient. A recent series of papers concerning spore germination of the fern, Onoclea sensibilis L., addresses this gap in our knowledge and could be highly relevant to studies of the mechanism of light regulated seed dormancy. Phytochrome-mediated germination of Onoclea requires the presence of Ca++ in the incubation medium and is reversibly inhibited by the Ca++ chelator EGTA (ethylene glycol-bis(B amino-ethyl ether)-N,N,N',N'-tetraacetic acid), lanthanum, and cobalt. Increasing the tissue concentration of Ca++ using ionophores permitted germination in the dark. Inhibitors of Ca++ action (calmodulin inhibitors) also reversibly inhibited germination (Wayne and Hepler 1984). Increased concentration of Ca++ was observed within the spores 5 minutes after exposure to red light and was inhibited by far-red light (Wayne and Hepler 1985). No change in spore pH was observed in conjunction with light-stimulated germination. Artificially induced pH changes from pH 5.8 to 7.2 had no effect on germination (Wayne et al. 1986). These studies provide the first evidence for a step between light exposure and its developmental expression in a structure analogous to a dormant seed. This potentially opens up the study of phytochrome mediated germination to the widely known, but still incompletely defined, area of calcium regulated biochemistry (Campbell 1983). Integration between new knowledge of phytochrome regulated germination and the contribution of other ion fluxes (see above) must also be attempted.

CHEMICAL STRUCTURE - PHYSIOLOGICAL ACTIVITY STUDIES

The chemical structural features which are necessary for dormancy-breaking activity are ill defined. Aldehydes, ketones, alcohols, carboxylic acids, esters, and nitriles of various structures are capable of breaking seed dormancy (French and Leather 1979; Taylorson and Hendricks 1980/81; Adkins et al. 1985; French et al. 1986; Cohn et al. 1986, 1987). No easily perceivable trends in these data account for such a broad spectrum of active substances. In the absence of rigorous biochemical studies, one can only speculate about their modes of action within the framework of research summarized above.

"DRY-AFTERRIPENING"

Many seeds will spontaneously lose dormancy during storage in the unimbibed state at ambient temperatures. While this process is commonly called "dry-afterripening", the term may not be physiologically accurate. If seeds are dehydrated to very low moistures (5% or less) under low humidity conditions in the absence of heating, the process is significantly inhibited[2] (Quail and Carter 1969; De Miguel and Soriano 1974; Tokumasu et al. 1975, 1981; Baskin and Baskin 1979; Ellis et al. 1983). Seed drying under these conditions does not apparently reduce seed viability or vigor. These data should provide the stimulus to pursue the relevance of chemical oxidations to the loss of dormancy in the dehydrated state. The only recent study related to the mechanism of "dry-afterripening" shows a correlation between inorganic phosphate levels and the intensity of dormancy. More dormant lines of wild oats contained lower whole seed Pi which increased with "dry-afterripening" (Quick and Hsiao 1984). The physiological significance of these observations awaits further study.

CONCLUDING REMARKS

Seed dormancy is truly a state of developmental arrest or suspended animation compared to germinating seeds. Net nucleic acid synthesis (i.e. that not required for repair operations), protein synthesis, and vigorous intermediary metabolism do not appear to occur. Therefore, the most pertinent philosophical as well as operational question to be kept in mind is: how are these active processes of a germinating seed coordinately suspended during dormancy? Furthermore, what imposes such complete control over the organism and still allows survival, sometimes for many years, in the imbibed state in soil? What regulatory events underlie the orderly resumption of metabolic activity as the seed emerges from the dormant state? And how do we avoid confusing the biochemistry of dormancy release with germination chemistry? It is my feeling that coarse controls such as cellular pH, redox state, regulation of ion fluxes, and sulfhydryl status merit more experimental attention.

The biggest limitation to the understanding of seed dormancy, however, is not our lack of knowledge. The critical mass of suitably-trained scientists required for efficient evaluation of hypotheses does not exist. We either have seed biologists lacking the depth of biochemistry required for such a project or biochemists who do not appreciate the nuances of seed behavior (i.e. the need for "inhouse" seed production, reliable harvesting procedures, rigorous attention to seed storage conditions, etc). For example, it required more than fifteen years for a challenge to the pentose shunt hypothesis to be published in the literature. Seed dormancy research has often been bootlegged with other projects or addressed as a hobby project. I believe progress will come when it is realized that dormancy work requires intensive effort and dependable, long-term funding (of course!). The importance of seed dormancy in agriculture at every level clearly justifies such a vigorous approach. If the current pace of research continues as it has over the past 50 years, I think we will be very lucky to find the answers needed to benefit agricultural production in our lifetime.

LITERATURE CITED

Ackerson, R.C. 1984. Regulation of soybean embryogenesis by abscisic acid. J. Exp. Bot. 35:403-413.

Adkins, S.W., and J.D. Ross. 1981. Studies in wild oat seed dormancy. II. Activities of pentose phosphate pathway dehydrogenases. Plant Physiol. 68:15-17.

Adkins, S.W., G.M. Simpson and J.M. Naylor. 1984a. The physiological basis of seed dormancy in Avena fatua. IV. Alternative respiration and nitrogenous compounds. Physiol. Plant. 60:234-238.

Adkins, S.W., J.M. Naylor and G.M. Simpson. 1984b. The physiological basis of seed dormancy in Avena fatua. V. Action of ethanol and other organic compounds. Physiol. Plant. 62:18-24.

Adkins, S.W., G.M. Simpson and J.M. Naylor. 1984c. The physiological basis of seed dormancy in Avena fatua. VI. Respiration and the stimulation of germination by ethanol. Physiol. Plant. 62:148-152.

Adkins, S.W., G.M. Simpson and J.M. Naylor. 1985. The physiological basis of seed dormancy in Avena fatua. VII. Action of organic acids and pH. Physiol. Plant. 65:310-316.

Amen, R.D. 1968. A model of seed dormancy. Botan. Rev. 34:1-31.

Ap Rees, T. 1980. Assessment of the contributions of metabolic pathways to plant respiration. IN D.D. Davies, ed., The Biochemistry of Plants, Vol 2. Academic Press, New York. pp 1-29.

Baskin, J.M., and C.C. Baskin. 1979. Effect of relative humidity on afterripening and viability in seeds of the winter annual Draba verna. Botan. Gaz. 140:284-287.

Behl, R., and W. Hartung. 1986. Movement and compartmentation of abscisic acid in guard cells of Valerianella locusta: Effects of osmotic stress, external H+-concentration and fusicoccin. Planta 168:360-368.

---

[2]Leopold, A.C., and M.A. Cohn, in preparation.

Bewley, J.D., and M. Black. 1982. Physiology and biochemistry of seeds. 2. Viability, dormancy and environmental control. Springer-Verlag, Berlin. 375 p.

Bogatek, R., and A. Rychter. 1984. Respiratory activity of apple seeds during dormancy removal and germination. Physiol. Veg. 22:181-191.

Brooks, C.A., K.S. Yu and C.A. Mitchell. 1985. Salicylhydroxamic acid potentiates germination of Waldmann's Green lettuce seed. Plant Physiol. 79:386-388.

Busa, W.B. 1986. Mechanisms and consequences of pH-mediated cell regulation. Annu. Rev. Physiol. 48:389-402.

Campbell, A.K. 1983. Intracellular Calcium: Its Universal Role as Regulator. John Wiley and Sons, New York.

Cocucci, S.M., A. Ranieri and G. Zocchi. 1986. Potassium-dependent increase in RNA and protein synthesis in the early phase of incubation of the thermodormant Phacelia tanacetifolia seeds. Plant Physiol. 80:891-894.

Cohn, M.A., D.L. Butera and J.A. Hughes. 1983. Seed dormancy in red rice. III. Response to nitrite, nitrate, and ammonium ions. Plant Physiol. 73:381-384.

Cohn, M.A., and L. Castle. 1984. Dormancy in red rice. IV. Response of unimbibed and imbibing seeds to nitrogen dioxide. Physiol. Plant. 60:552-556.

Cohn, M.A., and J.A. Hughes. 1986. Seed dormancy in red rice. V. Response to azide, cyanide, and hydroxylamine. Plant Physiol. 80:531-533.

Cohn, M.A., L.A. Chiles and J.A. Hughes. 1986. New class of dormancy-breaking chemicals. Plant Physiol. S-80:21.

Cohn, M.A., K.J. Boullion and L.A. Chiles. 1987. Structure-activity studies of dormancy-breaking compounds in red rice. Plant Physiol. (in press).

De Miguel, L.C., and A. Soriano. 1974. The breakage of dormancy in Datura ferox seeds as an effect of water absorption. Weed Res. 14: 265-270.

Dziewanowska, K., and S. Lewak. 1982a. Hydrogen cyanide and cyanogenic compounds in seeds. IV. Metabolism of hydrogen cyanide in apple seeds under conditions of stratification. Physiol. Veg. 20:165-170.

Dziewanowska, K., and S. Lewak. 1982b. Hydrogen cyanide and cyanogenic compounds in seeds. V. Effects of cyanide and azide on germination of apple embryos in relation to their dormancy. Physiol. Veg. 20:171-177.

Ellis, R.H., T.D. Hong and E.H. Roberts. 1983. Procedure for the safe removal of dormancy from rice seed. Seed Sci. Technol. 11:77-112.

Esashi, Y., S. Wakabayashi, Y. Tsukada and S. Satoh. 1979a. Possible involvement of the alternative respiration system in the ethylene-stimulated germination of cocklebur seeds. Plant Physiol. 63:1039-1043.

Esashi, Y., Y. Ohhara, M. Okazaki and K. Hishinuma. 1979b. Control of cocklebur seed germination by nitrogenous compounds: nitrite, nitrate, hydroxylamine, thiourea, azide and cyanide. Plant Cell Physiol. 20:349-361.

Esashi, Y., Y. Sakai, R. Ushizawa and S. Tazaki. 1979c. Catalase is not involved in control of germination of cocklebur seeds. Aust. J. Plant Physiol. 6:425-429.

Esashi, Y., Y. Sakai and R. Ushizawa. 1981a. Cyanide-sensitive and cyanide-resistant respiration in the germination of cocklebur seeds. Plant Physiol. 67:503-508.

Esashi, Y., K. Kusuyama, S. Tazaki and N. Ishihara. 1981b. Necessity of a balance between CN-sensitive and CN-resistant respirations for germination of cocklebur seeds. Plant Cell Physiol. 22:65-71.

Esashi, Y., H. Komatsu, N. Ishihara and K. Ishizawa. 1982a. Dormancy and impotency of cocklebur seeds. VIII. Lack of germination responsiveness in primarily dormant seeds to cyanide, azide, anoxia and chilling. Plant Cell Physiol. 23:41-47.

Esashi, Y., H. Komatsu, R. Ushizawa and Y. Sakai. 1982b. Breaking of secondary dormancy in cocklebur seeds by cyanide and azide in combination with ethylene and oxygen, and their effects on cytochrome and alternative respiratory pathways. Aust. J. Plant Physiol. 9:97-111.

Evans, M.L. 1985. The action of auxin on plant cell elongation. CRC Crit. Rev. Plant Sci. 2:317-366.

Finkelstein, R.R., K.M. Tenbarge, J.E. Shumway and M.L. Crouch. 1985. Role of ABA in maturation of rapeseed embryos. Plant Physiol. 78:630-636.

Foley, M.E. 1986. Effect of fusicoccin and gibberellic acid on primary dormant Avena fatua caryopses. Physiol. Plant. 67:690-694.

French, R.C., and G.R. Leather. 1979. Screening nonanal and related volatile flavor compounds on the germination of 18 species of weed seed. J. Agric. Food Chem. 27:828-832.

French, R.C., P.T. Kujawski and G.R. Leather. 1986. Effect of various flavor related compounds on germination of curly dock seed (Rumex crispus) and curly dock rust (Uromyces rumicis). Weed Sci. 34:398-402.

Fuerst, E.P., M.K. Upadhyaya, G.M. Simpson, J.M. Naylor and S.W. Adkins. 1983. A study of the relationship between seed dormancy and pentose phosphate pathway activity in Avena fatua. Can. J. Bot. 61:667-670.

Hendricks, S.B., and R.B. Taylorson. 1974. Promotion of seed germination by nitrate, nitrite, hydroxylamine and ammonium salts. Plant Physiol. 54:304-309.

Hendricks, S.B., and R.B. Taylorson. 1975. Breaking of seed dormancy by catalase inhibition. Proc. Natl. Acad. Sci. USA 72:306-309.

Hendricks, S.B., and R.B. Taylorson. 1980. Reversal by pressure of seed germination promoted by anesthetics. Planta 149:108-111.

Jones, J.F., and M.A. Hall. 1981. The effect of ethylene on quantitative and qualitative aspects of respiration during the breaking of dormancy of Sperua arvensis L. seeds. Ann. Bot. 48: 291-300.

Karssen, C.M., D.L.C. Brinkhorst-van der Swan, A.E. Breekland and M. Koornneef. 1983. Induction of dormancy during seed development by endogenous abscisic acid: studies on abscisic acid deficient genotypes of Arabidopsis thaliana (L.) Heynh. Planta 157:158-165.

Khan, A.A., and C. Samimy. 1982. Hormones in relation to primary and secondary dormancy. IN A.A. Khan, ed., The Physiology and Biochemistry of Seed Development, Dormancy and Germination. Elsevier Biomedical Press, Amsterdam. pp 203-241.

Koornneef, M., G. Reuling and C.M. Karssen. 1984. The isolation and characterization of abscisic acid-insensitive mutants of Arabidopsis thaliana. Physiol. Plant. 61:377-383.

Kovacs, M.I.P., and G.M. Simpson. 1976. Dormancy and enzyme levels in seeds of wild oats. Phytochem. 15:455-458.

Kuo, W.H-J. 1981. Physiological studies on the grain dormancy of rice (Oryza sativa L.). Mem. College Agric. Natl. Taiwan Univ. 21:1.

Kuo, W.H-J., and C. Chu. 1983. No relation between catalase and dormancy of rice. J. Agric. Assoc. China 123:13-20.

Lacroix, L.J., and A.S. Jaswal. 1967. Metabolic changes in afterripening seed of Prunus cerasus. Plant Physiol. 42:479-480.

Lacroix, L.J., and A.S. Jaswal. 1973. Lipid and sugar metabolism during the afterripening of sour cherry embryos. Can. J. Bot. 51:1267-1270.

Marre, E. 1979. Fusicoccin: A tool in plant physiology. Annu. Rev. Plant Physiol. 30: 273-288.

Metzger, J.D. 1983. Role of endogenous plant growth regulators in seed dormancy of Avena fatua. II. Gibberellins. Plant Physiol. 73: 791-795.

Moolenaar, W.H. 1986. Effects of growth factors on intracellular pH regulation. Annu. Rev. Physiol. 48:363-376.

Olusuyi, S.A. 1973. Investigations of some respiratory enzymes in relation to seed dormancy in barley. Ph.D. Thesis. University of Reading.

Palevitch, D., and T.H. Thomas. 1976. Enhancement by low pH of gibberellin effects on dormant celery seeds and embryo-less half seeds of barley. Physiol. Plant. 37:247-252.

Peiser, G.D., T-T. Wang, N.E. Hoffman, S.F. Yang, H-W. Liu and C.T. Walsh. 1984. Formation of cyanide from carbon 1 of 1-aminocyclopropane-1-carboxylic acid during its conversion to ethylene. Proc. Natl. Acad. Sci. USA 81: 3059-3063.

Perino, C., E. Simind-Cote and D. Come. 1984. Effects of potassium cyanide and salicylhydroxamic acid on breaking of dormancy and respiratory activity of apple (Pyrus malus L.) embryos. C.R. Acad. Sci. Paris. Series III. 299:249-251.

Quail, P.H., and O.G. Carter. 1969. Dormancy in seeds of Avena ludoviciana and A. fatua. Aust. J. Agric. Res. 20:1-11.

Quick, W.A., and A.I. Hsiao. 1984. Changes in inorganic phosphate and seed germinability during afterripening of wild oats. Can. J. Bot. 62: 2469-2471.

Roberts, E.H. 1969. Seed dormancy and oxidation processes. IN H.W. Woolhouse, ed., Dormancy and Survival. Soc. Exp. Biol. Symp. 23:161-192. Academic Press, New York.

Roberts, E.H. 1973. Oxidative processes and the control of seed germination. IN W. Heydecker, ed., Seed Ecology. Butterworths, London. pp. 189-218.

Roberts, E.H., and R.D. Smith. 1977. Dormancy and the pentose phosphate pathway. IN A.A. Khan, ed., The Physiology and Biochemistry of Seed Dormancy and Germination. Elsevier Biomedical Press, Amsterdam. pp. 385-410.

Satoh, S., and Y. Esashi. 1980. No contribution of the pentose phosphate pathway in dormancy-breaking of cocklebur seeds. Physiol. Plant. 48:243-246.

Simmonds, J.A., and G.M. Simpson. 1971. Increased participation of pentose phosphate pathway in response to afterripening and gibberellic acid treatment in caryopses of Avena fatua. Can. J. Bot. 49:1833-1840.

Simmonds, J.A., and G.M. Simpson. 1972. Regulation of the Krebs cycle and pentose phosphate pathway activities in the control of dormancy of Avena fatua. Can. J. Bot. 50:1041-1048.

Singh, S.P., and L.G. Paleg. 1984a. Low temperature induction of hormonal sensitivity in genotypically gibberellic acid insensitive aleurone tissue. Plant Physiol. 74:437-438.

Singh, S.P., and L.G. Paleg. 1984b. Low temperature induced GA_3 sensitivity of wheat. II. Changes in lipids associated with the low temperature induced GA_3 sensitivity of isolated aleurone of wheat. Plant Physiol. 76:143-147.

Stillwell, W., and P. Hester. 1983. Kinetin increases water permeability of phosphatidylcholine lipid bilayers. Plant Physiol. 71: 524-530.

Stillwell, W., and P. Hester. 1984. Kinetin blocks abscisic acid - phosphatidylethanolamine channels in lipid bilayers. Z. Pflanzenphysiol. 114:65-76.

Taylorson, R.B., and S.B. Hendricks. 1973. Promotion of seed germination by cyanide. Plant Physiol. 52:23-27.

Taylorson, R.B., and S.B. Hendricks. 1980/81. Anesthetic release of seed dormancy - an overview. Isr. J. Bot. 29:273-280.

Thomas, T.H., and D.F. Sambrooks. 1985. Possible control of gibberellin induced release of temperature-dependent primary dormancy in seeds of celery (Apium granvelens L.) by transmembrane ion fluxes. Plant Growth Regulation 3:191-199.

Tokumasu, S., M. Kato and F. Yano. 1975. The dormancy of seed as affected by different humidities during storage in Brassica. Japan. J. Breed. 25:197-202.

Tokumasu, S., F. Kakihara and M. Kato. 1981. The change of dormancy of seeds stored in dessicators and/or harvested fruits in cruciferous crops. J. Japan. Soc. Hort. Sci. 50:208-214.

Upadhyaya, M.K., G.M. Simpson and J.M. Naylor. 1981. Levels of glucose-6-phosphate and 6-phosphogluconate dehydrogenases in the embryos and endosperms of some dormant and nondormant lines of Avena fatua during germination. Can. J. Bot. 59:1640-1646.

Upadhyaya, M.K., J.M. Naylor and G.M. Simpson. 1982. The physiological basis of seed dormancy in Avena fatua L. I. Action of the respiratory inhibitors sodium azide and salicylhydroxamic acid. Physiol. Plant. 54:419-424.

Upadhyaya, M.K., J.M. Naylor and G.M. Simpson. 1983. The physiological basis of seed dormancy in Avena fatua. II. On the involvement of alternative respiration in the stimulation of germination by sodium azide. Physiol. Plant. 58:119-123.

Wayne, R., and P.K. Hepler. 1984. The role of calcium ions in phytochrome-mediated germination of spores of Onoclea sensibilis L. Planta 160:12-20.

Wayne, R., and P.K. Hepler. 1985. Red light stimulates an increase in intracellular calcium in the spores of Onoclea sensibilis. Plant Physiol. 77:8-11.

Wayne, R., D. Rice and P.K. Hepler. 1986. Intracellular pH does not change during phytochrome mediated spore germination in Onoclea. Devel. Biol. 113:97-103.

Wood, A., and L.G. Paleg. 1972. The influence of gibberellic acid on the permeability of model membrane systems. Plant Physiol. 50:103-108.

Yu, K.S., C.A. Mitchell, S. Yentur and H.A. Robitaille. 1979. Cyanide insensitive, salicylhydroxamic acid-sensitive processes in potentiation of light-requiring lettuce seeds. Plant Physiol. 63:121-125.

THE RELEASE OF MULTIPLE DORMANCY AND METABOLIC RESPONSES TO SCARIFICATION IN INDIAN RICEGRASS SEEDS

Miller B. McDonald, Jr.[1]

ABSTRACT

Indian ricegrass, Oryzopsis hymenoides (Roem. and Shult.) Ricker, is an important forage crop in the western United States. Seeds of this species are dormant at harvest and even following several years of storage. This study revealed that Indian ricegrass seeds possessed a multiple dormancy governed by both the seed coat and embryo. Seed coat dormancy was relieved by acid scarification while embryo dormancy was overcome by addition of exogenous GA_3 or cytokinin to scarified but not intact seeds. Despite the promotive influence of scarification on releasing dormancy, acid scarification culminated in a 60% reduction in soluble proteins, increased seed exudates with increased scarification time, and delayed protein synthesis. Scarified seeds also showed greater levels of fungal contamination which could be controlled by fungicide application. Suggested methods for enhancing Indian ricegrass seed germination utilizing organic permeation of GA_3 application of a 40% maneb dust to scarified seeds are suggested.

INTRODUCTION

Indian ricegrass [Oryzopsis hymenoides (Roem. & Shult.) Ricker] is a native perennial bunchgrass common to the western United States and Canada. It thrives best on foothills and plains, especially in well-aerated rocky or sandy soils. It is an excellent forage crop (Rogler 1960), resistant to heavy grazing (Stoddart and Wilkinson 1938), and capable of controlling wind erosion (Bohmont and Lang 1957). Furthermore, because Indian ricegrass seeds are high in protein and fat content, they are popular feed of livestock and rodents (Hafenrichter et al. 1968). Indian ricegrass has the potential to be an important candidate for revegetation programs of depleted lands due to its adaptations to dry, infertile areas.

Several trial seedings have been attempted by governmental agencies and have failed. These poor results apparently stem from inadequate germination due to an inherent seed dormancy. Since 1934 (Huntamer 1934), methods for improving Indian ricegrass germination have been studied. To date, the only successful treatments are scarification (chemical or mechanical abrasion of the seed coat) and/or stratification (moist, cold treatment) of the seeds for extended periods (Huntamer 1934, Clark and Bass 1970).

Considering the potential agronomic importance of this crop, further studies of the germination mechanism of Indian ricegrass are warranted. This report is a synopsis of four papers (McDonald 1976, McDonald and Khan 1977, McDonald and Khan 1978, McDonald and Khan 1983) which examined causes of dormancy in Indian ricegrass seeds. Several new practical methods to enhance its field performance and germination are suggested.

MATERIALS AND METHODS

Seeds

Seeds of Indian ricegrass were obtained soon after harvest during the years 1969-1974 from Ralph M. Warner, Orchard Colorado. One-year-old seeds were used for all studies. In germination studies, 2-year-old seeds were included for comparison.

Acid Scarification and Hormone Treatments

One-year-old seed lots were scarified by treating 15 g of intact seeds in 200 mL concentrated H_2SO_4 for various times ranging from 0 to 45 min at $25^{\circ}C$. Two-year-old seed lots (seeds stored 2 years after harvest) were scarfied by treating 15 g of intact seeds in 200 mL of 67% H_2SO_4. Scarified seeds were washed thoroughly with running tapwater followed by distilled water and then air-dried for 24 hr. Scarified seeds for each experiment came from the same lot to limit reported variation in germination (Plummer and Frischknecht 1952). Seeds which were not scarified are referred to as intact.

---

[1] Professor, Department of Agronomy, The Ohio State University, Columbus, Ohio 43210.

Germination Studies

Fifty seeds (0.25 g) were placed in 9 cm petri dishes with two discs of Whatman No. 1 filter paper and 5.0 mL of the appropriate test solution. Each experiment had two to four replicates. Seeds were soaked for 72 hr in constant light at 25°C unless otherwise noted and germination was defined as visible growth of the embryonic axis. All solutions contained 50 mg·L^{-1} chloramphenicol.

Water and ^{3}H-Gibberellic Acid Uptake Studies

Water uptake was determined by weighing 100 intact and scarified Indian ricegrass seeds prior to soaking. The seeds were placed in 9 cm petri dishes lined with two layers of Whatman No. 1 filter paper moistened with 5.0 mL distilled water and soaked for specified times up to 24 hr at 25°C. After each period, the seeds were removed, blotted dry, and reweighed. The change in weight due to water uptake was calculated and expressed as mg change in weight per seed. The results are the mean of two replicates.

^{3}H-Gibberellic acid uptake was determined by placing 1-year-old intact and scarified Indian ricegrass seeds (0.5 g) in 9 cm petri dishes lined with two layers of Whatman No. 1 filter paper moistened with 5.0 mL of 5 x 10^{-6} M ^{3}H-GA$_3$ (Gibberellin-A-3, 4-^{3}H, Specific activity 1 mCi 1 x 10^{-6} M, New England Nuclear) containing 6 μCi 1 x 10^{-3} L. The seeds were placed in ^{3}H-GA$_3$ for specified times up to 24 hr at 25°C and washed in distilled water following soaking. An additional treatment designated intact-scarified (I-S) included seeds which were soaked in ^{3}H-GA$_3$ prior to scarification, washed and then scarified for 20 min in concentrated H$_2$SO$_4$. All seed samples were homogenized in a mortar containing 3.0 mL dioxane counting solution (50 g napthalene, 10 g 2,5-diphenyloxazole and 0.3 g 1,4-bis[2-(5-phenyloxazolyl)]-benzene in 1 L dioxane). The mortar was washed with 2.0 mL of the dioxane counting solution. The total 5.0 mL homogenate was placed in a liquid scintillation counting vial containing 5.0 mL of 10% Cabosil in dioxane providing a 5% Cabosil counting medium. The vials were cooled, placed in a Nuclear-Chicago Unilux II-A liquid scintillation counter and counts per minute determined. The results are the mean of two replicates.

Tetrazolium Test

For the tetrazolium test, 100 Indian ricegrass seeds were soaked for 14 hr to activate the dehydrogenase enzymes (Assoc. Off. Seed Anal. 1970). The seeds were placed in 9 cm petri dishes containing two discs of Whatman No. 1 filter paper and 5.0 mL of 1% triphenyl tetrazolium chloride. The petri dishes were transferred to an incubator at 35°C for 4 hr. At the end of this period, the plates were removed and the seeds sliced through the embryo to detect formazan. Seed halves which contained no red color were returned to the tetrazolium solution and incubated for 4 additional hr at 35°C in the dark and reevaluated. The results are the mean of two replicates.

Enzyme Studies

RNase and Isospecies

Fifty seeds (0.25 g) were ground in ice-cooled mortars in 2.0 mL of 30 x 10^{-3} M Tris-HCl, pH 7.6, 20% sucrose, 1 x 10^{-3} M magnesium acetate and 50 x 10^{-3} M KCl. After washing with 1.0 mL of buffer, the combined homogenate (3.0 mL) was centrifuged at 23,000 x g for 15 min at 4°C, and the supernatant used for RNase determinations. The enzyme was assayed by the method of Bex (1972). Isospecies were resolved by a procedure adapted from Bex (1972) and Wilson (1969). Seeds (0.25 g) were homogenized in 4.0 mL of buffer mixture as above. Supernatant containing 75 x 10^{-6} L RNase extract was layered on top of a 2.5% acrylamide stacking gel, pH 6.9, and a 7.5% acrylamide running gel containing 0.5 x 10^{-6} L of dialyzed yeast RNA. Electrophoresis was conducted at 4 x 10^{-3} Amps per tube in 50 x 10^{-3} M Tris-glycine buffer, pH 8.3, at 4°C. After electrophoresis, the gels were washed with distilled water and incubated at 37°C in 10 x 10^{-3} L of a solution containing 50 x 10^{-3} M KCl and 50 x 10^{-3} M potassium acetate, pH 4.0, for 30 min. Gels were stained with 0.2% toluidine blue in 0.1% acetic acid, pH 3.0. After washing the gels thoroughly, they were destained in 5% acetic acid. Cathodic RNase isozymes appeared as clear bands against a deep blue background. The zymograms are typical of at least three electrophoretic runs.

Protein Studies

Free Amino Acids

Free amino acids were determined in the supernatant of the protein precipitates by the method of Clark (1964). The optical density was determined at 570 nm. Results were expressed as ng amino acid/mg dry weight using glycine as the standard and are the mean of two replicates.

Soluble Protein

Fifty seeds were removed from petri dishes after each soaking period and homogenized in an ice cooled mortar containing 10 mL 0.05 M phosphate buffer, pH 6.1. Homogenate was centrifuged at 23,500 x g for 10 min at $4^{o}C$ and the supernatant collected. Soluble protein in 1×10^{-3} L of supernatant was determined by the method of Lowry et al. (1952). Optical density was determined after 30 min at 550 nm. Results were expressed as μg protein/mg dry weight using bovine serum albumin as the standard. Results are the mean of four replicates.

^{14}C-Leucine Incorporation

After various soaking times, 50 intact and scarified Indian ricegrass seeds were placed in 2.0 mL of appropriate hormone solution and 1.0×10^{-6} Ci $_3$L-(U-^{14}C) leucine (348×10^{-3} Ci 10^{-3} M, Radiochemcial Centre, Amersham). Seeds were incubated for 2 hr at $25^{o}C$, removed from solution, washed with distilled water, and homogenized in cooled mortars in 3.0 mL 0.2 M NaCl. The homogenate (6.0 mL) was centrifuged at 12,000 x g for 10 min at $4^{o}C$, supernatant collected, and the pellet suspended in 4.0 mL of 0.2 M NaCl and centrifuged again at 12,000 x g for 10 min at $4^{o}C$. This supernatant was combined with the first making a total volume of 10 mL.

Supernatant (1.0 mL) was added to 2.0 mL 0.2 M NaCl and 2.5 mL 15% trichloroacetic acid and the soluble protein precipitated for 1 hr at $4^{o}C$. The precipitate was collected on 2.4 cm GF/A Whatman glass fiber filters and washed with 20 mL 15% trichloroacetic acid. The filters were placed in liquid scintillation vials and dried for 1 hr in a forced-air oven preheated to $75^{o}C$. Vials were cooled, 10 mL toluene counting solution [5 g 2,5-diphenyloxazole + 0.3 g 1,1-bis 2-(5-phenyloxazolyl) benzene in 1 L toluene]

added, and the samples counted in a liquid scintillation counter. Results are the mean of four replicates.

Seed Leachates

Intact Indian ricegrass seeds were scarified for 15, 30, 45, and 60 min in concentrated H_2SO_4, thoroughly rinsed with tapwater, and allowed to air-dry for 24 hr. Two hundred scarified seeds from each treatment were placed in test tubes containing 10 mL distilled water and allowed to soak for 1/2, 2, 4, 8, and 24 hr. Seed leachates were determined with a Yellow Springs Instrument Model 31 conductivity cell (cell constant of 1.0 reciprocal cm). All values were expressed as $\mu mhos/g$ seed dry weight. Results are an average of four replicates and the experiment was repeated once.

Permeation, Fungicide and Standard Germination Studies

Gibberellic acid and maneb were permeated into scarified Indian ricegrass seeds according to the procedure described by Khan et al. (1973). Seeds were soaked in 100 mL acetone solutions for 90 min, the solutions decanted and the seeds dried under vacuum for 30 min. Seeds dusted with fungicides were placed in Erlenmeyer flasks containing appropriate fungicide and agitated until thoroughly covered with the compound. Specific concentrations of maneb were prepared using talc as the inert material. Since maneb degrades during storage (Bontoyan and Looker 1973), only recent commercial preparations were used. Optimum temperatures for standard germination were determined using germinators set for the desired temperature ($\pm 1^{o}C$) and 95% relative humidity. For alternating temperatures, the high temperature was for 8 hr and the low temperature for 16 hr. Germination was evaluated according to the Rules for Testing Seeds (Assoc. Off. Seed Anal. 1970).

RESULTS

Seed Coat Effects

Seed coat influence on Indian ricegrass germination was studied. Seeds were treated to remove, weaken, or alter their seed coats. Following each treatment, germination was examined (table 1). Scarification with H_2SO_4 was the most

effective treatment for eliciting germination from intact seeds. Freezing (-20°C) and thawing (43°C) for various periods failed to increase germination above the control. Boiling the seeds rendered them ungerminable. Exposing the seeds to several enzymes or combination of enzymes (pectinase, cellulase, tyrosinase) failed to increase germination. Similarly, treatments with H_2O_2, leaching in running tap water, treatment with various organic solvents, and soaking in O_2 bubbled water did not improve germination. Exogenous applications of GA_3 and kinetin were unsuccessful in promoting germination of intact seeds.

Table 1. Influence of various treatments on the germination of intact 2-year-old Indian ricegrass seeds after 72 hr soaking.

Treatment	Before treatment	After treatment
	-----% Germination-----	
Scarification (67% H_2SO_4, 40 min)	5	67
Freeze (-20°C)-Thawing (43°C)	5	6
Boiling (0.5 to 6.0 min)	4	0
Enzymes (24 to 72 hr)		
Pectinase	4	4
Cellulase	5	4
Tyrosinase	5	4
Cellulase + Tyrosinase	4	5
H_2O_2 (0.01 to 6.00%)	5	3
Leaching (24 to 120 hr)	5	▪
Organic solvents (0 to 60 min)		
Ethanol	4	0
Ether	4	9
Chloroform	6	1
Acetone	5	7
Hormonal treatments		
GA_3 (10 x 10^{-6} M)	5	5
Kinetin (10 x 10^{-6} M)	5	6
ABA (10 x 10^{-6} M)	5	2
O_2 bubbled water	3	2

L.S.D. (0.05) = 5

Seed coats of Indian ricegrass play a significant role in determining whether a seed will germinate. As removal of the seed coats by scarification resulted in germination, a study was conducted to determine if seed coats were impermeable to water and other solutes. Scarified seeds became fully imbibed after 4 hr soaking while intact seeds continued to imbibe water during the 24 hr soaking period (fig. 1). These results indicated that seed coats and associated external structures provide a substantial, although not total, barrier to water uptake. Since GA_3 and kinetin failed to enhance germination of intact seeds, a study was conducted to determine whether GA_3 penetrates seed coats. Labeled GA_3, like water, readily entered scarified seeds and demonstrated maximal incorporation within 4 hr soaking (fig. 1). Intact seeds continued to incorporate labeled GA_3 up to 24 hr soaking. In another study, intact seeds soaked in labeled GA_3 were then scarified with H_2SO_4 and the amount of radioactivity associated with various seed parts determined. Relatively small amounts of label were found in internal seed structures (seed minus seed coats) suggesting that exogenous GA_3 is located principally in the seed coats of intact seeds.
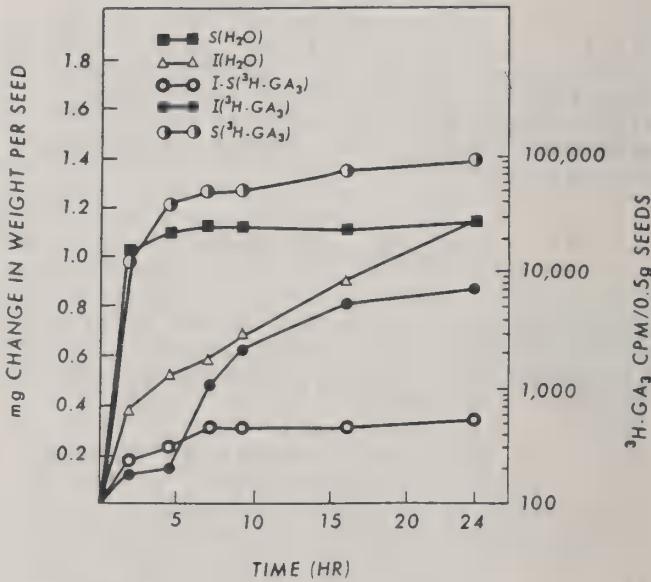
Figure 1. Water and ^3H-GA_3 uptake by intact (I), scarified (S), and intact-scarified (I-S) 1-year-old Indian ricegrass seeds.

In a similar fashion, the permeability of a large molecule was also examined. Tetrazolium chloride reacts with hydrogen ions made available through the activity of dehydrogenase enzymes to form an insoluble red pigment, formazan. Embryos from intact seeds failed to produce formazan (0%) while embryos from scarified seeds readily produced the pigment (99%). However, embryos from intact seeds were shown to be viable when they were returned to the tetrazolium solution following excision. Within 4 hr, formazan formation occurred (97%).

The GA$_3$ and tetrazolium experiments suggest that Indian ricegrass seedcoats, while slowly permeable to water, are impermeable to larger molecules.

Since H$_2$SO$_4$ scarification was the most successful means of eliciting germination, further studies of this treatment were conducted. Seeds of various ages were treated with concentrated H$_2$SO$_4$ at different times to determine the optimum length of treatment for germination. Maximum germination varied with seed age; older seeds requiring less scarification than freshly harvested seeds (fig. 2).
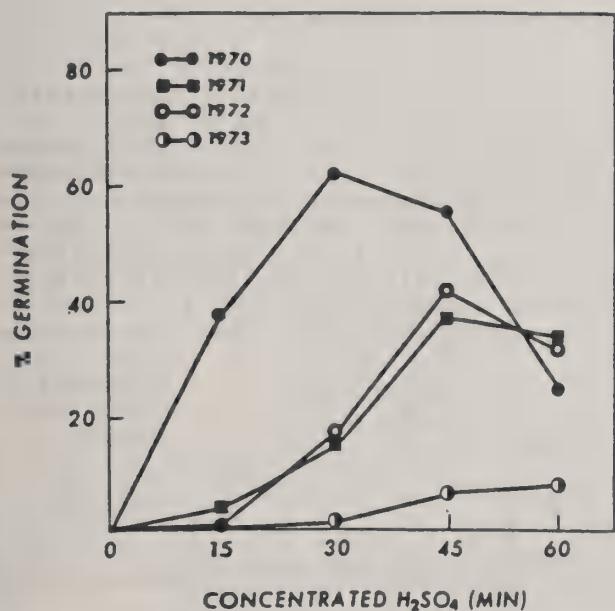
Figure 2. Influence of concentrated H$_2$SO$_4$ on the germination of 1, 2, 3, and 4-year-old Indian ricegrass seeds.

In another study, 1-year-old Indian ricegrass seeds were stored at 25°C and 65% relative humidity and at 4°C and 50% relative humidity for one year (table 2). Following this period, the seeds were scarified with concentrated and 67% H$_2$SO$_4$, washed, and germinated. Seeds stored at 25°C and 65% relative humidity germinated at a higher level than seeds stored at 4°C and 50% relative humidity. These results suggest that storage at high temperature and high relative humidity produced certain physiological changes which allow maximum germination from shorter scarification treatments.

The effects of various hormones on dormancy release in scarified 1-year-old and 2-year-old Indian ricegrass seeds were studied. Gibberellic acid and kinetin enhanced while abscisic acid inhibited germination of scarified seeds (table 3). Hormones did not affect intact seed germination. Gibberellic acid and kinetin stimulated germination in 1-year-old seeds to a greater extent compared to 2-year-old seeds.

These studies clearly show that scarification enhances Indian ricegrass seed germination and that exogenous hormone application further increases this response. These data suggest that both a seed coat and embryonal dormancy exist in Indian ricegrass seeds. Yet, despite these promotive responses after scarification and hormone applications, little is known concerning the fate of the metabolic machinery following scarification. Specific studies examining various components of protein synthesis following scarification in the presence and absence of exogenous hormones were established.

Table 2. Influence of storage for 1 year at 4°C and 50% relative humidity (RH) versus storage at 25°C and 65% relative humidity on germination after 72 hr soaking of 1-year-old intact Indian ricegrass seeds following scarification.

Storage Condition	Scarification treatment	Acid Treatment (min)			
		20	40	60	80
		-------% Germination------			
4°C, 50% RH	67% H$_2$SO$_4$	0	4	5	9
25°C, 65% RH	67% H$_2$SO$_4$	0	9	17	19
4°C, 50% RH	Conc. H$_2$SO$_4$	4	5	5	2
25°C, 65% RH	Conc. H$_2$SO$_4$	7	22	8	0
L.S.D. 0.05 = 3					

Table 3. Influence of various exogenous hormonal treatments on the germination of 1- and 2-year-old intact and scarified Indian ricegrass seeds after 72 hr soaking.

| | 1-year | | 2-year | |
Treatment	Intact	Scarified	Intact	Scarified
	------------------% Germination------------------			
H_2O	0	31	5	67
10×10^{-6} M GA_3	0	65	5	76
10×10^{-6} M Kinetin	0	54	6	72
10×10^{-6} M ABA	0	1	2	2
L.S.D. 0.05 = 4				

Protein Synthesis Following Acid Scarification

Free Amino Acids

Free amino acid levels in intact seeds were unaffected by water soaking for various times or by hormonal treatments (fig. 3). In scarified seeds, free amino acid levels increased with increased soaking time. Free amino acid levels were enhanced by GA_3 treatment while ABA treatment inhibited these levels compared to the control after 72 hr soaking.

Soluble Protein

Intact seed soluble protein levels were high and unaffected by hormonal treatments (fig. 4). Acid scarification reduced soluble protein levels by nearly 60%. No differences in hormonal treatments were observed until 48 hr soaking. At 48 and 72 hr, GA_3 enhanced while ABA inhibited the soluble protein content compared to the water control.
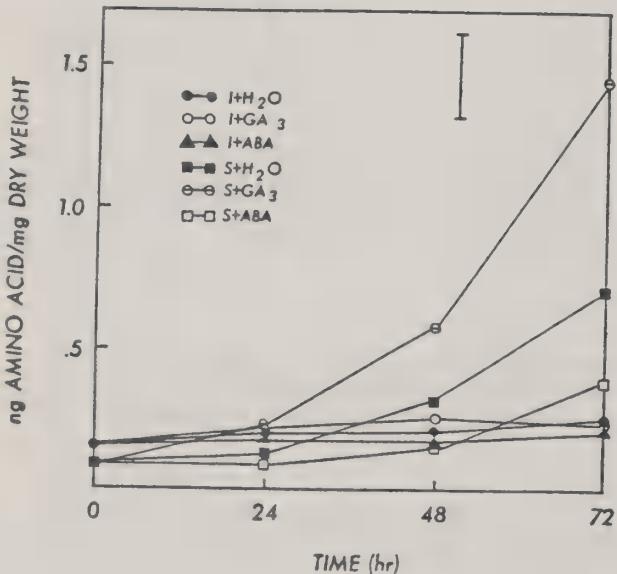
Figure 3. Soluble amino acid levels of intact (I) and scarified (S) 1-year-old Indian ricegrass seeds as influenced by 10×10^{-6} M GA_3 and 10×10^{-6} M ABA during soaking. Vertical bar denotes L.S.D. (0.05) to compare any two treatment means.
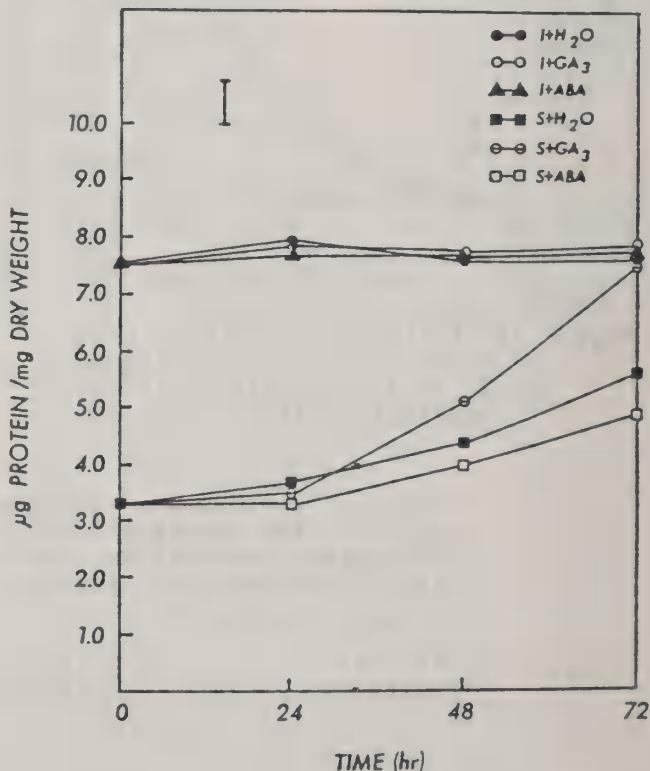
Figure 4. Soluble protein levels of intact (I) and scarified (S) 1-year-old Indian ricegrass seeds as influenced by 10×10^{-6} M GA_3 and 10×10^{-6} M ABA during soaking. Vertical bar denotes L.S.D. (0.05) to compare any two treatment means.

^{14}C-Leucine Incorporation

A marked increase in the leucine incorporation of intact seeds at 24 hr soaking compared to the 0 hr control was observed and this effect was not altered by GA_3 or ABA (fig. 5). The ability to incorporate leucine into protein decreased in all intact seed treatments following 48 and 72 hr of soaking. Acid scarification markedly reduced the ability of Indian ricegrass seeds to incorporate leucine into protein for up to 24 hr of soaking. At this time, GA_3 slightly enhanced the leucine incorporation over the control. A sharp increase in leucine incorporation occurred at 48 hr of soaking in water and ABA treated seeds. Gibberellin A_3 application, in contrast, showed no additional increase in leucine incorporation at 48 hr. A decrease in leucine incorporation occurred in all scarified treatments after 72 hr soaking. The amount incorporated was much less than the intact, dormant seeds.
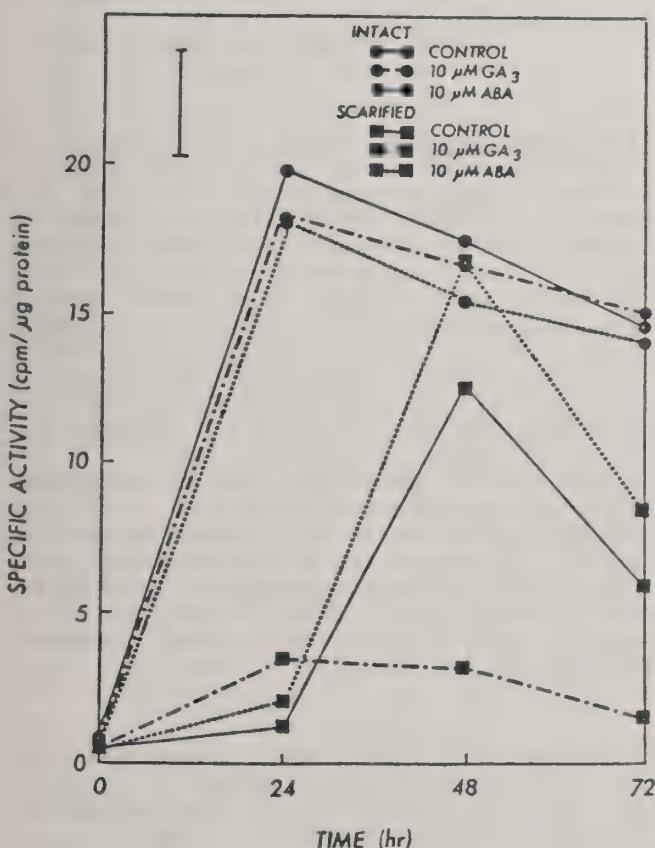
Figure 5. Incorporation of ^{14}C-leucine into soluble protein of 1-year-old intact and scarified Indian Ricegrass seeds as influenced by 10×10^{-6} M GA_3 and 10×10^{-6} M ABA during soaking. Vertical bar denotes L.S.D. (0.05) to compare any two treatment means.

RNase Activity

While quantitative differences occurred in isozymes of RNase in intact seeds during soaking, only scarified seeds showed both quantitative and qualitative changes (fig. 6). Five isozymes (I_1 to I_4, I_7) were present in intact seeds at zero time and after 24 hr of soaking. Three of these (I_3, I_4, I_7) increased in intensity at 48 hr with no further increase at 72 hr. In scarified seeds, no isozymes were detectable at 24 hr. At 48 hr, an isozyme (I_4) appeared which increased in intensity after 72 hr at which time three new isozymes (I_5, I_6, and I_8) were present. When GA_3 was added, two isozymes (I_4, I_6) appeared at 48 hr and three (I_7 to I_9) at 72 hr. GA_3-treated seeds differed from untreated scarified seeds by having two new isozymes (I_7, I_9) present. A greater intensity was seen in two others (I_4, I_6). I_5 was absent in GA_3-treated scarified seeds. Only one isozyme (I_4) was found in ABA-treated scarified seeds and was less intense than its counterpart in untreated GA_3-treated seeds at 72 hr.

Seed Leachates

Intact Indian ricegrass seeds or those scarified for various times showed similar patterns of seed leachate response (fig. 7). However, the severity of scarification also influenced the degree of exudate loss. Seeds scarified for 0, 15, or 30 min exhibited 75% of the quantity of exudates lost from seeds scarified for 45 or 60 min. After 30 min scarification, leachate levels increased with increasing scarification time.

Permeation, Fungicides, and Standard Germination

Previous studies have shown that Indian ricegrass seeds exhibit two forms of seed dormancy: a mechanical restraint imposed by the lemma and palea and an embryo dormancy. Embryo dormancy is transient and does not contribute to dormancy following one year of storage. However, seed coat dormancy persists and requires removal of the indurated lemma and palea by sulfuric acid. Even though scarification results in greater germination than intact seeds, this process culminates in delayed protein synthesis and greater leakage of exudates from scarified seeds. While the previous

DECREASING INTENSITY

H₂O (I) H₂O (S)   H₂O (I) GA₃ (I) ABA (I) H₂O (S) GA₃ (S) ABA (S)

0 hr

24 hr

48 hr

72 hr
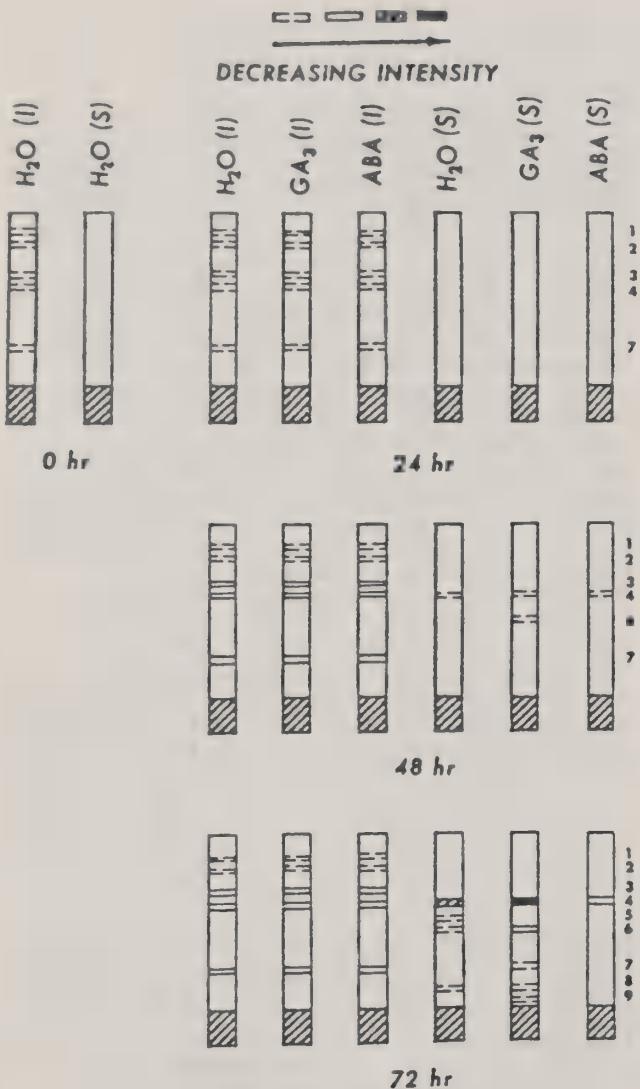
Figure 6. Isoribonucleases of intact (I) and scarified (S) Indian ricegrass seeds as influenced by time of soaking and treatment with 10 x 10⁻⁶ M GA₃ and 10 x 10⁻⁶ M ABA.

Figure 7. Seed leachate levels of 1-year-old Indian ricegrass seeds scarified for various times as expressed by conductivity (μmhos/g seed). Vertical bar denotes L.S.D. (0.05) to compare any two treatment means.

studies have contributed to a greater understanding of dormancy mechanisms governing Indian ricegrass seeds, they have not provided applied recommendations for improving standard germination tests for these seeds nor have they suggested a practical method to treat seeds for enhanced stand establishment. The following studies were designed to address these issues.

Scarified Indian ricegrass seeds (concentrated H_2SO_4, 35 min) were germinated on blue blotters using standard AOSA germination procedures (AOSA 1970). Three storage fungi (_Rhizopus_ _nigricans_, _Aspergillus_ _niger_,

and _Aspergillus_ _terreus_) were common contaminates of these germination tests. To reduce this contamination, several common fungicides (PCNB, Vitavax, captan, thiram, Botran, Granox, and maneb) were screened for fungistatic properties. Of the fungicides studied, only maneb was effective for complete control of storage fungi. The optimum concentration of maneb applied as a dust for scarified Indian ricegrass seed germination was determined in the presence and absence of 0.1×10^{-3} M GA₃ (table 4). At concentrations above 60%, maneb exhibited phytotoxic properties while at concentrations below 40%, maneb failed to control contaminating microorganisms. These results demonstrated that scarified seeds soaked in 0.1×10^{-3} M GA₃ and treated with a 40-60% maneb dust enhanced germination to 76% after 7 days.

Permeation of GA₃ and maneb using acetone as a carrier into scarified seeds resulted in a promotion of germination by GA₃ but poor fungal control by maneb (table 5). These results suggested that GA₃ was permeated by acetone while maneb was not.

Table 4. Germination after 7 days of scarified Indian ricegrass seeds treated with various concentrations of maneb in the presence and absence of 0.1 x 10^{-3} M GA_3.

Conc. Maneb	Treatment	
	H_2O	0.1×10^{-3} M GA_3
	----% Germination---	
H_2O	21	37
H_2O + Talc	37	52
20%	47	78
40%	61	64
60%	64	76
80%	31	22

L.S.D. 0.05 = 7

Table 5. Germination after 7 days of scarified Indian ricegrass seeds permeated by acetone with 0.1 x 10^{-6} M GA_3 and various concentrations of maneb.

Concentration maneb	% Germination
H_2O	25
Acetone	41
Acetone + 0.1 x 10^{-3} M GA_3	73
0.07%	74
0.13%	73
0.25%	73
0.50%	74
1.00%	70

L.S.D. 0.05 = 3

Optimum temperatures for germination of scarified seeds have yet to be determined. This study showed maximum germination of scarified seeds at 25, 30, and 20-30°C after 4 and 7 days (table 6). The most rapid seedling growth of scarified Indian ricegrass seeds was noted at 30°C. AOSA Rules for Testing Seeds (1970) recommend Indian ricegrass seeds be prechilled in soil or moistened blotters for 4 weeks, then placed at 15°C for an additional 21 days. The success of this procedure was compared to the scarification method. After 49-days, germination of intact seeds in soil (4%) and blotters (6%) was substantially lower than germination of scarified seeds after 7 days (90%).

Table 6. Mean percentage germination of scarified Indian ricegrass seeds imbibed in 0.1 x 10^{-6} M GA_3 and dusted with 40% maneb at various temperatures.

Temperature C	4 days	7 days
	---% Germination---	
5	0	0
10	0	0
15	0	54
20	13	91
25	85	89
30	87	90
35	36	57
20-30	87	91
20-35	61	87

L.S.D. 0.05 = 5

DISCUSSION

Seed Coat and Embryonal Dormancy

Amen (1968) suggested that seed coats of many species are capable of inhibiting germination. They function as permeability barriers, the site of inhibitors, or mechanical constraints to embryo growth. These considerations were investigated in this study. Of the many methods which have been reported to alter seed coat dormancy, the only one which proved effective with Indian ricegrass was acid scarification (table 1).

Huntamer (1934) showed that the indurated lemma and palea of Indian ricegrass seeds are permeable to water. Subsequently, Fendall (1964) found that intact Indian ricegrass seeds imbibed water although their rate of imbibition was slower than dehulled seeds. This study confirms these reports and shows that Indian ricegrass seed coats do present a substantial permeability barrier to water during the first 16 hr soaking period (fig. 1).

As GA_3 and kinetin promoted germination in scarified but not intact seeds (table 3), it is possible that larger molecules encounter penetration resistance from the seed coats. The use of labelled GA_3, and presumably other hormones, can be introduced into intact seeds to a limited extent. Similarly, results with tetrazolium salts also suggested that large molecules encounter a seed coat resistance. The nature of this permeability barrier is not known.

These results show that the seed coats of Indian ricegrass influence germination. The response of scarified Indian ricegrass seeds to exogenous hormones suggests that germination in these seeds is governed by a postharvest embryo dormancy as well. This conclusion is derived from the following results: 1.) Older seeds required less scarification for maximal germination (fig. 2); 2.) Storage of seeds at low temperature and relative humidity delayed physiological changes which occurred during storage of seeds at higher temperature and relative humidity (table 2); and 3.) Both GA_3 and kinetin caused marked enhancements of germination in 1-year-old scarified seeds but produced only small increases in germination of 2-year-old scarified seeds (table 3).

Post-harvest dormancy is common in several cereal grains (Barton 1965) and after-ripening results in increased gibberellin synthesis in oat (Avena sativa L.) (Simpson 1965) and barley (Hordeum vulgare L.) (Khan and Waters 1969) seeds. Promotion of germination by GA_3 in 1-year-old scarified seeds may be due to an inherent deficiency of endogenous gibberellins. The lack of any appreciable effect by exogenous GA_3 in 2-year-old scarified seeds (table 3) may be due to increased GA synthesis during the after-ripening period. The promotive effect of both GA_3 and kinetin on germination of scarified Indian ricegrass seeds is similar to that in pear (Pyrus malus L.) embryos (Khan and Heit 1969) and some species of barley (Pollock 1959).

These studies show that dormancy imposed either by mechanical (seed coat) or physiological (embryonal) blocks can lead to a reduction in seed biochemical activity. Intact and scarified seeds demonstrated quantitative and qualitative differences in protein and enzymatic activities as well as responses to exogenous hormones.

Protein Synthesis Following Acid Scarification

An increase in free amino acids, soluble proteins, and ribonuclease was observed for seeds exposed to exogenous GA_3. ABA treatment inhibited these responses (figs. 3, 4, and 6). Interestingly, protein synthesis as determined by ^{14}C-leucine incorporation into soluble proteins demonstrated that intact seeds possessed the greatest specific acitivity and that ABA treated seeds incorporated more leucine than either control or GA_3 treated scarified seeds (fig. 5). These results suggest that GA_3 (and presumably endogenous GA) stimulates while ABA inhibits proteolytic activity during germination and seedling growth. Thus, a greater amino acid pool size is present in scarified (germinating) seeds which is further increased by exogenous GA_3 resulting in reduced incorporation of ^{14}C-leucine (figs. 3 and 5). The opposite effect was observed for ABA treated seeds. Such results are consistent with other observations which have shown that ABA treatment decreased the amino acid pool size by nearly 50% in peas (Pisum sativum L.) (Yomo and Varner 1973). Gibberellin A_3 is also known to enhance while ABA inhibits protease acitivity (Jacobsen and Varner 1967). Free amino acid levels of scarified and intact seeds at 0 and 24 hr of soaking were low and not markedly different (fig. 3). However, leucine incorporation was almost 20-fold less in scarified seeds compared to intact seeds at 24 hr of soaking (fig. 5). This difference in leucine incorporation into protein suggests an initial deleterious effect of acid scarification on the protein synthesizing apparatus. This effect is neither permanent nor long-lived since free amino acid levels and increased leucine incorporation were detected after 48 hr of soaking (figs. 3 and 5).

Since acid scarification removes the testa and probably a considerable portion of the endosperm, a large decrease in soluble proteins (fig. 4) might be attributed to a loss of non-embryonic portions of the seed. A fixed level of soluble protein in intact seeds during the soaking period is suggestive of little or no synthesis or mobilization of storage proteins prior to germination and growth. Scarification of seeds also led to complete disappearance of five isozymes (I_1-I_4, I_7) of RNase (fig. 6) suggesting that they may be located in seed portions other than the embryo or are broken down as a result of scarification. Similar findings have been reported for peroxidase enzymes in which some isoperoxidases were lost as a consequence of acid scarification (McDonald and Khan 1978). Thus, soluble proteins and other solutes are most likely lost during scarification and during the initial stages of soaking. The leakage study demonstrated the loss of some compounds during the first 24 hr soaking (fig. 7). Scarification exacerbated this response. Some of these factors which are lost through leaching may be associated with the proper functioning of protein synthesis. A period of time may be required before protein synthesis can be reestablished.

The exact mechanism for reduction of soluble protein levels and delayed

protein synthesis in scarified Indian ricegrass seeds is not yet known. However, considering the aleurone layer location (immediately beneath the seed testa) and its well documented role in the early stages of hydrolytic enzyme synthesis, any damage to this tissue caused by acid scarification would clearly retard early hydrolysis of endospermic reserves and could affect the nutritive status of the growing embryo. The delay in protein synthesizing ability may be a manifestation of time-dependent germination occurred in scarified seeds, the 24 hr delay in amino acid incorporation, noted in scarified seeds compared to intact seeds (fig. 5) may be related to repair of the protein synthesizing apparatus, presumably in the aleurone layer, and replacement of soluble protein levels and other factors necessary for embryo growth (fig. 4).

Zemetra and Cuany (1984) offered another consideration when explaining the injury mechanism in Indian ricegrass seeds following acid scarification. They found a difference in lemma thickness, ranging from 42 to 76 x 10^{-6} m, in 12 cultivars of Indian ricegrass. They reported that greater acid damage was associated with decreased lemma thickness and proposed that determination of lemma thickness could be used as a criterion to assess the optimal durations of acid scarification to minimize seed injury.

Permeation, Fungicides and Standard Germination

These studies have clearly shown that acid scarification and addition of GA_3 enable complete and rapid germination of Indian ricegrass seeds. However, these procedures resulted in seed injury manifested by delayed protein synthesis (fig. 5), increased leakage of cellular constituents (fig. 7), and consequent severe fungal contamination. Table 6 demonstrated that maneb provided adequate control of microflora when applied as a dust to scarified seeds.

Several studies have shown that hormonal compounds and pesticides are permeated into seeds using organic solvents (Khan et al. 1973, Meyer and Mayer 1971, Tao and Khan 1974). Since simultaneous application of GA_3 and maneb to scarified Indian ricegrass seeds could reduce seed treatments required for germination and result in economic savings to seedsmen, this technique was studied. However, fungal contamination remained severe in scarified seeds permeated with maneb. It was concluded that maneb was not incorporated into seed tissues. This lack of maneb permeation is likely a consequence of its low solubility in organic solvents (Agriculture Canada 1973). The application of maneb to scarified seeds as a dust or slurry, either alone or in conjunction with GA_3, is suggested.

This study identifies methods to increase Indian ricegrass seed germination. Depending upon cost and equipment, any of the following procedures are recommended:

   o Obtain freshly harvested seeds and store for one year at 25°C, grade the seed according to size (McDonald 1976), scarify with concentrated sulfuric acid, and dust seeds with 40% maneb.

   o Obtain freshly harvested seeds, grade seeds according to size, scarify with concentrated sulfuric acid, permeate seeds with 0.1 x 10^{-6} M GA_3 via acetone and dust seeds with 40% maneb.

   o Obtain freshly harvested seeds, grade seeds according to size, scarify with concentrated sulfuric acid, treat seeds with a 0.1 x 10^{-6} M GA_3 and 40% maneb slurry.

These recommendations have been attempted in the field and the greenhouse (Zemetra and Cuany 1983). They found that concentrated sulfuric acid effectively increased greenhouse germination; GA_3 enhancing emergence of the freshly harvested seeds. Unfortunately, field studies did not produce this enhancement. Seeds which were acid scarified displayed decreases in field emergence. The weakened seed covering, further destroyed by freeze/thaw cycles over winter, was suggested as an explanation for this finding. Once the integrity of the seed covering is broken, soil pathogens can attack and kill the seeds.

Although optimum temperatures for germination of intact Indian ricegrass seeds have been reported to be 15 (Assoc. Off. Seed Anal. 1970) and 5-15°C (Clark and Bass 1970), this study has shown that optimum germination of scarified Indian ricegrass seeds can be obtained at 30°C after 7 days (table 6). Testing of scarified Indian ricegrass seeds, therefore, should be conducted on blotters at 3°C and the first and final counts obtained following 4 and 7 days, respectively.

Heretofore, the most reliable method for projecting stands of Indian ricegrass seeds has been the tetrazolium test. However, this technique fails to reveal dormancy. Although breeding procedures may ultimately eliminate Indian ricegrass seed dormancy, the scarification methods proposed suggest improved techniques for commercial processing and seed testing evaluation.

LITERATURE CITED

Amen, R. D. 1968. A model of seed dormancy. Bot. Rev. 34:1-31.

Agriculture Canada. 1973. Guide to the chemicals used for crop production. Information Canada, Ottawa. 542p.

Assoc. Off. Seed Anal. 1970. Rules for testing seeds. Proc. Assoc. Off. Seed Anal. 60(2):1-116.

Assoc. Off. Seed Anal. 1970. Tetrazolium Handbook. Contr. No. 29. 62p.

Barton, L. V. 1965. Seed dormancy: General survey of dormancy types in seeds and dormancy imposed by external agents. Encycl. Plant Physiol. 15:699-720.

Bex, J. H. M. 1972. Effects of abscisic acid on nucleic acid metabolism in maize coleoptiles. Planta 103:1-10.

Bohmont, B. L. and R. Lang. 1957. Some variations in morphological characteristics and palatability among geographic strains of Indian ricegrass. J. Range Manag. 10:127-131.

Bontoyan, W. R. and J. B. Looker. 1973. Degradation of commercial ethylene dithio-carbamate formulations to ethylenethiourea under elevated temperatures and humidity. Agr. Food Chem. 21:338-341.

Clark, D. C. and L. N. Bass. 1970. Germination experiments with seeds of Indian ricegrass, Oryzopsis hymenoides (Roem. and Schult.) Ricker. Proc. Assoc. Off. Seed Anal. 60:226-239.

Clark, J. M. 1964. Experimental biochemistry. W. H. Freeman and Co., San Francisco. 228p.

Fendall, R. K. 1964. An investigation into the site and cause of seed dormancy of Stipa viridula and Oryzopsis hymenoides. Ph.D. thesis, North Dakota Univ.

Hafenrichter, A. L., J. L. Schwendiman, H. L. Harris, R. S. MacLauchlan, and H. W. Miller. 1968. Grasses and legumes for soil conservation in the Pacific Northwest and Great Basin States. Agric. Handbook 339, Soil Conserv. Serv., USDA.

Huntamer, M. Z. 1934. Dormancy and delayed germination of Oryzopsis hymenoides. M. A. Thesis, State College of Washington.

Jacobsen, V. and J. E. Varner. 1967. Gibberellic acid-induced synthesis of protease by isolated aleurone layers of barley. Plant Physiol. 42:1596-1600.

Khan, A. A. and C. E. Heit. 1969. Selective effect of hormones on nucleic acid metabolism during germination of pear embryos. Biochem. J. 113:707-712.

Khan, A. A., K. L. Tao, and C. H. Roe. 1973. Application of chemicals in organic solvent to dry seeds. Plant Physiol. 52:79-81.

Khan, A. A. and E. C. Waters. 1969. On the hormonal control of postharvest dormancy and germination in barley seeds. Life Sci. 8:729-736.

Lowry, O. H., N. J. Rosebrough, A. L. Farr, and R. J. Nandall. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193:265-275.

McDonald, M. B., Jr. 1976. Improving the germination of Indian ricegrass. J. Seed Technol. 1:44-54.

McDonald, M. B., Jr. and A. A. Khan. 1977. Factors determining germination of Indian ricegrass seeds. Agron. J. 69:558-563.

McDonald, M. B., Jr. and A. A. Khan. 1978. Metabolic changes in Indian ricegrass seeds in relation to coat-imposed and embryonal dormancy. Agron. J. 70:829-835.

McDonald, M. B., Jr. and A. A. Khan. 1983. Acid scarification and protein synthesis during seed germination. Agron. J. 75:111-114.

Meyer, H. and A. M. Mayer. 1971. Permeation of dry seeds with chemicals: Use of dichloromethane. Science 171:583-584.

Plummer, A. P. and N. C. Frischknecht. 1952. Increasing field stands of Indian ricegrass. Agron. J. 44:285-289.

Pollock, J. R. A. 1959. Studies in barley and malt. XV. Growth substances and other compounds in relation to dormancy in barley. J. Inst. Brew. 65:334-337.

Rogler, G. A. 1960. Relation of seed dormancy of Indian ricegrass (Oryzopsis hymenoides (Roem. & Schult.) Ricker) to age and treatment. Agron. J. 52:470-473.

Simpson, G. M. 1965. Dormancy studies
in seed of _Avena fatua_. 4. The role of
gibberellin in embryo dormancy. Can J.
Bot. 43:793-816.

Stoddart, L.A. and K.J. Wilkinson. 1938.
Inducing germination in _Oryzopsis
hymenoides_ for range reseeding. Agron.
J. 30:763-768.

Tao, K. L. and A. A. Khan. 1974.
Penetration of dry seeds with chemicals
applied in acetone. Plant Physiol. 54:
956-958.

Wilson, C. M. 1969. Rapid staining
technique for detection of RNA after
polyacrylamide gel electrophoresis.
Anal. Biochem. 31:506-511.

Yomo, H. and J.E. Varner. 1973. Control
of the formation of amylases and
proteases in the cotyledons of
germination peas. Plant Physiol.
51:708-713.

Zemetra, R. S., C. Havstad, and R. L.
Cuany. 1983. Reducing seed dormancy in
Indian ricegrass (_Oryzopsis
hymenoides_). J. Range Manag. 36:239-
241.

Zemetra, R. S. and R. L. Cuany. 1984.
Variation in lemma thickness in Indian
ricegrass: Implications for dormancy,
scarification, and breeding. Crop Sci.
24:1082-1084.

SEED-COAT ANATOMY, HARDSEEDEDNESS, AND SCARIFICATION OF SMALL-SEEDED FORAGE LEGUMES

C. E. Townsend[1] and P. N. Miklas[2]

ABSTRACT

Proper seed scarification is essential for germination and stand establishment of many small-seeded forage legumes. Numerous methods have been used to reduce hardseededness including chemicals, mechanical scarification, heating, freezing, radiation, percussion, and enzymes. Mechanical scarification is probably the most common commercial treatment. Genetic as well as environmental factors influence the expression of hardseededness.

INTRODUCTION

Seeds that will not imbibe water and germinate in a favorable environment are referred to as impermeable or hardseeds. Although the hardseeded trait is found in a number of species, it is especially widespread in the Fabaceae. Depending on the species, hardseeds may or may not be a desirable character. For some species, hardseeds result in poor germination and subsequent stand establishment. Conversely, hardseeds are essential for the natural reseeding of some annual species. Hardseeds of commercially grown forage legumes have been a concern of plant scientists for years.

ANATOMY OF THE SEED COAT

The anatomy of the seed coat or testa is very similar for all members of the subfamily Papilionoideae which have been studied (Rolston 1978). A thin, noncellular layer, known as the cuticle, covers the entire surface of the seed coat. The various cellular components of the seed coat are differentiated from the outer integument of the ovule.

Macrosclereid Cells

Macrosclereid cells form the outermost cell layer of the seed coat. They are also known as malpighian, epidermal, palisade, or prism cells. The macrosclereid cells are oriented perpendicular to the seed surface. Generally, a macrosclereid cell has three distinct regions, i.e., the base

and lumen which are inward, the "light line," and the cap or dome which is outward. The "light line" extends along the outer periphery of the macrosclereid cells just below the caps. It occurs in an area where there is a change in the chemical composition of the cells which results in a difference in the refraction of light (Hamly 1932). The macrosclereid cell layer is generally thought to be the impermeable barrier to the imbibition of water.

Osteosclereid Cells

Osteosclereid cells form a single layer interior to the macrosclereid cell layer. They are also known as hourglass, columnar, pillar, or spool cells. Large intercellular spaces generally occur between the osteosclereid cells. The endosperm, a nutrient layer consisting of parenchyma cells, occurs beneath the osteosclereids.

Hilum

The hilum is the scar left by the detachment of the funiculus from the seed, and is composed of counterpalisade cells and macrosclereid cells. Therefore, the seed coat at the hilum differs from that at other locations on the seed surface.

Strophiole or Lens

The strophiole is a weak point in the macrosclereid cell layer and is visible as a small bump on the seed coat. It is located near the hilum on the side opposite the radicle and micropyle. The macrosclereid cells gradually become thinner and longer near the strophiole.

DEVELOPMENT OF THE HARDSEED COAT

Two apparently incompatible processes, the desiccation of the embryo and the development of an impermeable seed coat, occur during the ripening of legume seed such as that of white clover (_Trifolium_ _repens_ L.) and red clover (_T. pratense_ L.) (Hyde 1954). Ripening seeds dry rapidly until their moisture content reaches about 25%. Thereafter, moisture is lost more slowly until the epidermis becomes impermeable at a moisture content of about 14%. Additional drying of the seed occurs only by diffusion of water vapor through the hilar fissure which acts as a hygroscopic valve in the impermeable epidermis of the seed coat. The moisture content of hardseeds tends to be in equilibrium with the lowest relative humidity to which they have been exposed. If the seeds are then exposed to a higher relative humidity, the hilar fissure closes, excepting under conditions of a gradual increase in relative humidity wherein the hilar fissure remains open. The length of time that hardseeds remain impermeable increases as the degree of desiccation increases. Imbibition of water is controlled by the strophiole region after absolute impermeability is reached (Ballard 1973). When

---

[1]Research Geneticist, USDA, ARS, Crops Research Laboratory, 1701 Center Ave., Fort Collins, Colorado 80526.

[2]Research Associate, Colorado State University, Fruita Research Center, P.O. Box 786, Grand Junction, Colorado 81502.

hardseeds of the papilionate legumes become naturally permeable, imbibition occurs through the strophioles which have opened, possibly due to temperature fluctuation (Ballard 1973).

DISTRIBUTION OF THE HARDSEED TRAIT

Watson (1948) evaluated 21 introduced and native species of small-seeded forage legumes for hardseededness and noted that germinated or permeable seed for seven species (including alsike clover, T. hybridum L.; red clover, and yellow sweetclover, Melilotus officinalis Lam.) ranged from 61 to 98%; for six species (including purple-flowered alfalfa, Medicago sativa L.) ranged from 27 to 55%; and for eight species (including yellow-flowered alfalfa, M. falcata L.; white sweetclover, M. alba Medik.; and birdsfoot trefoil, Lotus corniculatus L.) ranged from 5 to 21%. Seeds that did not germinate were primarily hardseeds. Although a detailed examination of the 21 species showed variation in the structural and chemical (cutin, suberin, and cellulose, etc.) nature of the seed coat, no trait was consistently associated with an impermeable or permeable seed coat. Cicer milkvetch (Astragalus cicer L.) (Carleton et al. 1971) and crownvetch (Coronilla varia L.) (Brant et al. 1971) commonly have 80% or more hardseed. In more recent studies, selected progenies of cicer milkvetch differed significantly (P ≤ 0.05) for resistance to mechanical and sulfuric-acid scarification, but no difference was found among them for seed-coat anatomy (Miklas et al. 1987). Twenty-four hours after mechanical and acid scarification, hardseed content ranged from 12 to 77% and from 12 to 52%, respectively.

METHODS USED TO REDUCE HARDSEEDEDNESS

Various methods have been used to reduce hardseededness in the Fabaceae. These methods include chemicals, mechanical scarification, heating, freezing, radiation, percussion, and enzymes.

Chemicals

A variety of solvents including acetone, benzene, chloroform, hexane, anhydrous ether, petroleum ether, ethyl alcohol, and t-butyl alcohol were used to treat hardseeds of crownvetch (Brant et al. 1971). Although acetone, petroleum ether, ethyl alcohol, and t-butyl alcohol reduced hardseed content slightly, the results were not considered practical. In addition, these treatments caused a significant increase in rotted seed and a decrease in germination. Absolute ethyl alcohol was effective for treating impermeable seeds of species in the subfamily Caesalpinioideae, but was not effective for species in the Papilionoideae (Barton 1947). Seeds of the Mimosoideae occupied an intermediate position between those of the other two subfamilies.

Sulfuric acid, the most common chemical treatment, has also been used successfully to scarify seeds of many species (Barton 1965). The strophiole accounted for 75% of the area of water imbibition for cicer milkvetch seed following sulfuric-acid scarification (Miklas et al. 1987). Scanning electron microscopy showed that sulfuric acid dissolved the cuticle and exterior portions of the macrosclereids and formed a circular cavity which had a large groove at its base. Conversely, the hilum was the primary area of water imbibition in blue lupine (Lupinus angustifolius L.) seed following scarification with sulfuric acid (Burns 1959). Hamly (1932) observed that various areas of the seed coat of sweetclover imbibed water after scarification with sulfuric acid. Sulfuric acid may cause a significant increase in percentage of rotted seeds. Concentration, immersion time and agitation have a pronounced influence on the effect of the chemical to the seed coat and subsequent germination. Special attention must be given to the dangers involved while handling chemical scarifying agents.

Mechanical scarification

Mechanical scarification probably is the most common commercial treatment for impermeable seeds (Rolston 1978). Although mechanical scarification has successfully reduced the hardseed percentage of most small-seeded forage legumes, it usually damages some seeds, especially in the radicle-hypocotyl region. Carleton et al. (1971) utilized a quick-swell test to determine the effectiveness of mechanical scarification to seeds of cicer milkvetch. When 30 to 50% of the seeds imbibed water within 24 hours, they were considered to be properly scarified. Four of the most successful preliminary treatments for reducing the impermeability of crownvetch seed were compared (Brant et al. 1971). Percent germination for the control, hot water, liquid N, sulfuric acid, and mechanical scarification treatments was 16, 47, 65, 75, and 82, respectively. There was little difference among treatments for percent rotted seeds which ranged from 5 to 7.

Mechanical and sulfuric-acid scarification were equally effective in scarifying seeds for eight of 10 selected progenies of cicer milkvetch; i.e., 11 and 12%, respectively, on the 14th day of test (Miklas et al. 1987). There was no apparent reason for the differential response of the two progenies. The strophiole and seed tip (area of the seed coat farthest from the hilum) accounted for 98% of the area of imbibition following mechanical scarification. Similar results were found with sweetclover seeds (Hamly 1932; Hagon and Ballard 1970). Scanning electron microscopy revealed that the effect of mechanical scarification on the seed coat of cicer milkvetch varied from no effect to small scrapes and indentations, large cracks, and complete seed-coat removal. In general, mechanical and sulfuric-acid scarification were equally effective in scarifying seeds of crownvetch (Brant et al. 1971).

The selected progenies of cicer milkvetch also differed (P ≦ 0.05) for percentage germination following mechanical and sulfuric-acid scarification (Miklas et al. 1987). Percentage hardseed following mechanical scarification was significantly correlated (P ≦ 0.05) with seed traits such as length, width, volume, and weight (r = -0.91, -0.66, -0.88, and -0.82, respectively). Large seeds tended to be more easily scarified than small seeds. Seed density (weight/volume) was the only trait significantly correlated (r = 0.70) with hardseed percentage following sulfuric-acid scarification.

The seed coat of crownvetch differs slightly from that of other forage legume species in that the remnants of the inner integument are present and must be pierced before water will be imbibed (McKee et al. 1977). When the seed coat was pierced to a depth of 98 μm or more, all of the seeds germinated. Pressure on the hilum, strophiole, and micropyle during the piercing process did not make these structures permeable to water. According to Ballard (1976), however, the strophile and testa should be regarded as an integrated system because the mechanical properties of the remainder of the testa could influence the transmission of stress to the strophiole.

Heating

Both dry heat and moist heat (Lute 1928, Rincker 1954, Lunden and Kinch 1957, Brant et al. 1971) have been used to reduce hardseed percentage in many legume species. Hardseeds of alfalfa and red clover became permeable when heated for 4 min. at 104°C while those of sweetclover remained impermeable (Rincker 1954). Rincker also noted that the heat treatment which increased seed-coat permeability did not result in any visible abnormalities in the resulting seedlings. Heat treatments have to be carefully regulated or seed viability will be lost by overheating.

High, fluctuating temperatures (15-75°C) in both the field and laboratory improved the permeability of hardseeds of subterranean clover (T. subterraneum L.) and Lupinus varius L. (Quinlivan 1966). In subterranean clover, less than 20% of the viable seeds survived exposure to field temperatures in the absence of dormancy and impermeability (Quinlivan 1971). Hagon (1971) demonstrated that the action of temperature fluctuation on the seed coat of subterranean clover was confined to the strophiole. Soil surface temperatures in the field greater than 50° to 55°C were required to reduce the impermeability of hardseeds of Stylosanthes humilis H.B.K. and S. hamata (L.) Taub. (McKeon and Mott 1982). In the laboratory the hardseed content of S. humilis, S. hamata, S. scabra Vog., and S. viscosa was reduced up to 70% by agitating the seed on metal plates at temperatures of 140° to 150°C for 15 to 30 s (Mott 1979). After impermeable seeds were rendered permeable through natural or artificial means, the imbibition of water occurred most frequently at the strophiole rather than at random sites over the surface of the seed coat.

Two types of impermeability were found in hardseeds of L. varius (Quinlivan 1968). In one type, the hardseeds (conditionally hard) had a moisture content above 10% (dry wt basis) and slowly softened in a humid environment. Imbibition of moisture occurred at random sites over the seed coat, but generally not at the hilum or strophiole. In the second type, hardseeds (absolutely hard) had a moisture content below 8.5% and would not soften when placed in a moist environment. If exposed to daily fluctuation in temperature between 15° and 65°C, the impermeable coat fractured at the strophiole.

When crownvetch seed was immersed in water at temperatures of 50°, 75°, and 100°C for 0.25, 0.50, 1.0, and 5.0 min., percentage hardseed was reduced significantly (P ≦ 0.01) at the 100°C treatment (Brant et al. 1971). Most seeds, however, were killed when treated at 100°C for 1.0 min. or more. After crownvetch seed was immersed in 100°C water for 30 s with agitation and then dipped in cool water (15°C), mean germination at 14 days increased from 17% for the control to 49% for the treated seed.

Freezing

Impermeable seeds of alfalfa and sweetclover were made permeable by treating with liquid air (-190°C) (Busse 1930). Treatment of hardseeds of sweetclover (Barton 1947) and crownvetch (Brant et al. 1971) in liquid nitrogen (-196°C) reduced hardseed content considerably. Hardseed content of crownvetch, however, was not adequately reduced when treated at -80°C in a freezer.

Radiation

Different sources of radiation have been tested for their potential as hardseed reducing treatments. They are as follows: infrared, radio frequency, gas plasma, and microwaves. These methods are equally effective and are relatively inexpensive to administer (Rincker 1954, Nelson et al. 1964, Nelson et al. 1968, Stetson and Nelson 1972, Works 1964). Nelson et al. (1968) treated 27 seed lots from five varieties of alfalfa with infrared and radio frequency and both treatments reduced hardseed from about 50 to 5%. Stetson and Nelson (1972) compared a radiofrequency (RF) dielectric heater, a hot air oven, and a microwave oven for effectiveness in treating hardseeds of three alfalfa varieties. Although the three methods were equally effective in overcoming hardseededness, the RF treatment was the fastest. These treatments were more effective when seed moisture content was low and less effective when moisture content was high. For all sources of radiation, heat was the factor that increased permeability. If properly used, these methods cause less damage than mechanical scarification and might provide an alternative to mechanical scarification.

Percussion

Percussion was used successfully by Hamly (1932) and Barton (1947) to increase the seed permeability of several species. The strophiole is selectively affected by percussion and results in water imbibition (Hamly 1932).

Enzymes

The enzymes hemicellulase and pectinase reduced impermeable seeds of crownvetch from 68 to 48 and 54%, respectively (Brant et al. 1971).

ENVIRONMENT

Environmental conditions, particularly temperature and moisture, during seed maturation affects the development of hardseed coats. For example, the hardseed content of alfalfa produced in high temperature areas such as southern California is usually less than 20% (Gunn 1972). When produced in the cooler environments of Washington, hardseed content is usually 40 to 50%. Dexter (1955) noted that alfalfa seed produced at low altitudes had a lower hardseed content than seed lots produced at high altitudes. If the weather is moist during seed maturation, the seeds of some species may germinate in the pod before the hardseed coat develops.

Day length during seed maturation of the winter annual, facultative, long-day legume (Ononis sicula Guss.) affected the permeability of the seed coat (Gutterman and Heydecker 1973). A reduced day length during the last eight days of ripening increased seed-coat permeability.

In studies with crimson clover (T. incarnatum L.) James and Bancroft (1951) reported that higher levels of calcium in the soil increased hardseed content, while higher levels of potassium decreased hardseed content. Phosphorus had no significant effect on hardseed content. Soil fertility had little, if any, effect on the production of hardseeds (Rolston 1978).

SEED LONGEVITY

Hardseed coats may dramatically increase seed longevity. Wilton et al. (1978) germinated seeds of alfalfa (M. sativa and M. falcata) that ranged in age from 23 to 70 years. The seed had been stored in unheated and uninsulated buildings at Belle Fourche, SD, and Mandan, ND. Two seed lots of M. falcata germinated 48 and 27% after 66 and 68 years of storage, respectively. One seed lot of M. sativa germinated 7% after 70 years and a second seed lot germinated 39% after 62 years of storage. In general, seeds of M. falcata retained their viability longer than M. sativa. The increased longevity of M. falcata seeds was believed due to their greater content of hardseeds.

Germination of cicer milkvetch seed increased while hardseed content decreased through 14 years of storage (Hafenrichter et al. 1965). We found that the viability of seeds from over 50 polycross progenies of cicer milkvetch was excellent following 10 years of storage in an unheated and uninsulated building (unreported studies). The germination of some progenies, however, was substantially better than that of other progenies. Priestley et al. (1985) evaluated published data dealing with seed longevity for 92 species and estimated the length of their half-viability period.

GENETICS

Genetic as well as environmental factors influence the expression of hardseededness. Aitken (1939) showed that the impermeable seed of subterranean clover was due to the suberized thickening on the outer surface of the malpighian cells. The degree of hardseededness was conditioned by genotype, environment, and subsequent dehydration of the seed.

Although James (1949) reported no evidence for the inheritance of seed-coat impermeability in crimson clover, Bennett (1959) increased hardseededness of selected populations from 1 to 61% in nine years of mass screening. In addition to seed-coat impermeability, there is a high-temperature dormancy for seed germination in crimson clover (Knight 1965). Hardseed content in Persian clover (T. resupinatum L.) was increased through selection for eight generations from 0.5 to 63% (Weihing 1962).

The hardseeded trait from Vicia cordata Wulf. was transferred by interspecific hybridization to the softseeded and more agronomically desirable V. sativa L. (Donnelly 1971). Inheritance of the hardseeded trait in several F_2 populations of this cross indicated that the data were best interpreted by a two-gene model, A-B- (Donnelly et al. 1972). The A gene behaved as a simple dominant for hardseed and the B gene was dominant for softseed when the A locus was homozygous recessive, aa. The double recessive genotype (aabb) was hardseeded.

Hardseededness, an undesirable trait, was dominant to softseededness in blue lupine and was controlled by a single pair of alleles (Forbes and Wells 1968). Gladstones (1970) reported that seed-coat impermeability in blue, yellow (L. luteus L.), and white (L. albus L.) lupines was inherited as a single dominant gene. There was 5 and 56% hardseed in M. sativa and M. falcata, respectively, while their hybrid, M. media, had 20% hardseed (Mijatovic 1971). Inheritance of seed permeability in sweetclover was complex (White and Stevenson 1948). Permeability was associated with sunken, brownish, and irregular shaped spots on the seed coat. It was not determined if the spots were due to a disease organism.

Because cicer milkvetch progenies with larger seeds tended to be more easily scarified than those with smaller seeds, Miklas et al. (1987) suggested that seed weight would be the easiest seed trait to use when selecting and breeding for increased permeability following mechanical scarification.

Populations of alfalfa and red clover plants derived from entire seed lots and from hardseeds in them were similar in fall growth habit and winter survival (Smith 1961). Therefore, it appears that the presence of hardseeds would not result in genetic drift, at least, for these two quantitatively inherited traits.

LITERATURE CITED

Aitken, Y. 1939. The problem of hard seeds in subterranean clover. Proc. Roy. Soc. Vict. N. S. 51:187-212.

Ballard, L. A. T. 1973. Physical barriers to germination. Seed Sci. and Technol. 1:285-303.

Ballard, L. A. T. 1976. Strophiolar water conduction in seeds of Trifolieae induced by action on the testa and non-strophiolar sites. Aust. J. Plant Physiol. 3:465-469.

Barton, L. V. 1947. Special studies on seed coat permeability. Contr. Boyce Thompson Inst. Plant Res. 14:355-362.

Barton, L. V. 1965. Dormancy in seeds imposed by the seed coat. pp. 727-745. In: W. Ruhland (ed.). Encyclopedia of Plant Physiology (Handbuch der Pflanzenphysiologie). XV: Part 2. Springer-Verlag, Berlin.

Bennett, H. W. 1959. The effectiveness of selection for the hard seeded character in crimson clover. Agron. J. 51:15-16.

Brant, R. E., G. W. McKee, and R. W. Cleveland. 1971. Effect of chemical and physical treatment on hard seed of Penngift crownvetch. Crop Sci. 11:1-6.

Burns, R. E. 1959. Effect of acid scarification on lupine seed impermeability. Plant Physiol. 34:107-108.

Busse, W. F. 1930. Effect of low temperatures on germination of impermeable seeds. Bot. Gaz. 89:169-179.

Carleton, A. E., R. D. Austin, J. R. Stroh, L. E. Wiesner, and J. G. Scheetz. 1971. Cicer milkvetch-seed germination, scarification and field emergence studies. Mont. Agric. Exp. Stn. Bull. 655. 21 pp.

Dexter, S. T. 1955. Alfalfa seedling emergence from seed lots varying in origin and hard seed content. Agron. J. 47:357-361.

Donnelly, E. D. 1971. Breeding hard-seeded vetch using interspecific hybridization. Crop Sci. 11:721-724.

Donnelly, E. D., J. E. Watson, and J. A. McGuire. 1972. Inheritance of hard seed in Vicia. J. Hered. 63:361-365.

Forbes, I., and H. D. Wells. 1968. Hard and soft seededness in blue lupine, Lupinus angustifolius L. Inheritance and phenotype classification. Crop Sci. 8:195-197.

Gladstones, J. S. 1970. Lupines as crop plants (review article). Field Crop Abstr. 23:123-148.

Gunn, C. R. 1972. Seed characteristics. In C. H. Hanson (ed.). Alfalfa Sci. Technol. Agronomy 15:677-687.

Gutterman, Y., and W. Heydecker. 1973. Studies of the surfaces of desert plant seeds. I. Effect of daylength upon maturation of the seedcoat of Ononis sicula Guss. Ann. Bot. 37:1049-1050.

Hafenrichter, A. L., R. B. Foster, and J. L. Schwendiman. 1965. Effect of storage at four locations in the west on longevity of forage seeds. Agron. J. 57:143-147.

Hagon, M. W. 1971. The action of temperature fluctuations on hard seeds of subterranean clover. Aust. J. Exp. Agric. Anim. Husb. 11:440-443.

Hagon, M. W., and L. A. T. Ballard. 1970. Reversibility of strophiolar permeability to water in seeds of subterranean clover (Trifolium subterraneum L.). Aust. J. Biol. Sci. 23:519-528.

Hamly, D. H. 1932. Softening of the seeds of Melilotus alba. Bot. Gaz. 93:345-375.

Hyde, E. O. C. 1954. The function of the hilum in some Papilionaceae in relation to the ripening of the seed and the permeability of the testa. Ann. Bot. 18:241-256.

James, E. 1949. The effect of inbreeding on crimson clover seed-coat permeability. J. Am. Soc. Agron. 41:261-266.

James, E., and T. A. Bancroft. 1951. The use of half-plants in a balanced incomplete block in investigating the effects of calcium, phosphorus, and potassium, at two levels each, on the production of hard seed in crimson clover. Agron. J. 43:96-98.

Knight, W. E. 1965. Temperature requirements for germination of some crimson clover lines. Crop Sci. 5:422-425.

Lunden, A. O., and R. C. Kinch. 1957. The effect of high temperature contact treatment on hard seeds of alfalfa. Agron. J. 49:151-153.

Lute, A. M. 1928. Impermeable seed of alfalfa. Colo. Agric. Exp. Stn. Bull. 326.

McKee, G. W., R. A. Peiffer, and N. N. Mohsenin. 1977. Seed coat structure in Coronilla varia L. and its relation to hard seed. Agron. J. 69:53-58.

McKeon, G. M., and J. J. Mott. 1982. The effect of temperature on the field softening of hard seed of Stylosanthes humilis and S. hamata in a dry monsoonal climate. Aust. J. Agric. Res. 33:75-85.

Mijatovic, M. 1971. A study of hard alfalfa seed. U.S.D.A. National Science Foundation. Contemp. Agric. 19(4):57-69.

Miklas, P. N., C. E. Townsend, and S. L. Ladd. 1987. Seed coat anatomy and the scarification of cicer milkvetch seed. Crop Sci. 27 (in press).

Mott, J. J. 1979. High temperature contact treatment of hard seed in Stylosanthes. Aust. J. Agric. Res. 30:847-854.

Nelson, S. O., L. E. Stetson, R. B. Stone, J. C. Webb, C. A. Pettibone, D. W. Works, W. R. Kehr, and G. E. VanRiper. 1964. Comparison of infrared, radiofrequency and gas-plasma treatments of alfalfa seed for hard-seed reduction. Trans. Am. Soc. Agric. Eng. 7:276-280.

Nelson, S. O., L. E. Stetson, and D. W. Works. 1968. Hard-seed reduction in alfalfa by infrared and radiofrequency electrical treatments. Trans. Am. Soc. Agric. Eng. 11:728-730.

Priestley, D. A., V. I. Cullinan, and J. Wolfe. 1985. Differences in seed longevity at the species level--a review. Plant, Cell and Environ. 8:557-562.

Quinlivan, B. J. 1966. The relationship between temperature fluctuations and the softening of hard seeds in some legume species. Aust. J. Agric. Res. 17:625-631.

Quinlivan, B. J. 1968. The softening of hard seeds of sand-plain lupin (Lupinus varius L.). Aust. J. Agric. Res. 19:507-515.

Quinlivan, B. J. 1971. Embryo dormancy in subterranean clover seeds. II. Its value relative to impermeability in field germination regulation. Aust. J. Agric. Res. 22:607-614.

Rincker, C. M. 1954. Effect of heat on impermeable seeds of alfalfa, sweetclover and red clover. Agron. J. 46:247-250.

Rolston, M. P. 1978. Water impermeable seed dormancy. Bot. Rev. 44:365-396.

Smith, D. 1961. Note on the growth characteristics of alfalfa and red clover plants derived from hard seeds and seeds of different sizes. Can. J. Plant Sci. 41:675-678.

Stetson, L. E., and S. O. Nelson. 1972. Effectiveness of hot air, 39-MH$_2$ dielectric and 2450-MH$_2$ microwave heating for hard-seed reduction in alfalfa. Trans. Am. Soc. Agric. Eng. 15:530-535.

Watson, D. P. 1948. Structure of the testa and its relation to germination in the Papilionaceae tribes Trifoliae and Loteae. Ann. Bot. 12:385-409.

Weihing, R. M. 1962. Selecting Persian clover for hard seed. Crop Sci. 2:381-382.

White, W. J., and R. M. Stevenson. 1948. Permeable seeded strains of sweetclover (Melilotus alba), their development and nature. Sci. Agric. 28:206-222.

Wilton, A. C., C. E. Townsend, R. J. Lorenz, and G. A. Rogler. 1978. Longevity of alfalfa seed. Crop Sci. 18:1091-1093.

Works, D. W. 1964. Infrared irradiation for water-impermeable seeds. Trans. Am. Soc. Agric. Eng. 7:235-237.

NATURAL AND ARTIFICIAL SCARIFICATION OF SEEDS WITH HARD COATS

Timothy E. Fulbright[1]

ABSTRACT

Natural seed scarification occurs through (1) passage through the digestive tract of animals, (2) abrasion by soil, (3) fire, (4) fungal and bacterial attack, (5) rodent activity, and (6) soil temperature fluctuations. Artificial scarification methods include mechanical, chemical, and hot and cold temperature treatments. The percentage of hard seeds may vary among lots of a species.

INTRODUCTION

Hard seed coats and/or coverings such as glumes, pericarps, and indurate lemmas and paleas inhibit germination of many range plant species. These structures may impose dormancy by (1) inhibiting water uptake and/or gas exchange by the embryo, (2) preventing embryo expansion, or (3) modifying the light reaching the embryo (Bewley and Black 1982). In this paper, "hard coat" includes all seed coverings that inhibit germination.

Ecological advantages conferred to plants by hard seed coats include increased longevity of seeds in the soil, protection of the embryo and endosperm against microbial attack, prevention of germination under environmental conditions unfavorable for seedling establishment, and improved seed dispersal. However, these structures make artificial plant establishment more difficult because germination may be delayed until long after the seeds are planted.

Seeds with hard coats must be scarified to germinate. Scarification softens, scratches, or ruptures the seed coat, thus increasing its permeability to water and/or gases and/or allowing embryo expansion. Scarification may occur naturally or artificially. The objectives of this paper are to discuss (1) how seeds with hard coats are scarified in nature, (2) effective methods of artificial scarification, and (3) factors that affect the percentage of hard seeds in a seed crop.

---

[1]Associate Professor of Range Management, College of Agriculture and Home Economics, Campus Box 156, Texas A&I University, Kingsville, Texas 78363.

NATURAL SCARIFICATION

Digestive Tract of Animals

Seeds of certain range plants are adapted for scarificaton in the digestive tract of birds and mammals. Fisher et al. (1959) reported that germination of honey mesquite (Prosopis glandulosa Torr.) seeds was 82, 69, and 25% after passage through the digestive tract of horses, steers, and ewes, respectively, compared to 26% for seeds left in the pods and not fed to the animals. Potter et al. (1984) fed prickly-pear (Opuntia sp.) seeds to cattle. Seeds exhibited 1.5 times greater percent germination after passage through the digestive tracts of the animals than seeds removed from ripe fruits. Passage through the digestive tract of baboons (Papio sp.) increased germination of Securinega virosa from 22% for fresh seeds to 97% for ingested seeds (Lieberman et al. 1979).

Dispersal by baboons increases the concentration of preferred food plants within the core area of their territory (Lieberman et al. 1979). Similarly, invasion of overgrazed rangeland by mesquite (Prosopis sp.) and other undesirable species such as huisache [Acacia farnesiana (L.) Willd.] (Scifres et al. 1982) and Macartney rose (Rosa bracteata Wendl.) (McCully 1951) has been attributed in part to scarification in the digestive tract and dissemination by animals.

Abrasion by Soil

Abrasion of seeds against soil particles may scarify coats and increase germination (Amen 1966). One hypothesis concerning how Indian ricegrass [Oryzopsis hymenoides (R. & S.) Ricker] dormancy is broken in nature is that seeds are naturally scarified by moving along the surface of sandy soils by saltation until the lemma and palea are broken by the abrasive action of sand grains (Young et al. 1983). However, Young et al. (1983) found that wear of the lemma and palea of this species from saltation is more associated with loss of viability than with germination enhancement.

Fire

Heat produced by fire may stimulate germination by cracking the seed coat. Stone and Juhren (1951) determined the effect of fire on seed germination of sugar bush (Rhus ovata Wats.) in a laboratory experiment. Seeds were planted in moist sand covered by a 5-cm layer of excelsior. Half of the excelsior was ignited. Germination of sugar bush seeds was 38% in the burned half and only 1% in the unburned half. Seeds heated for 5 minutes at 100° C had cracks in the water-impermeable second layer of the seed coat. These authors concluded that heating cracked the seed coat, which allowed entry of water.

Went et al. (1952) collected soil samples from burned and adjacent unburned areas in chapparal vegetation in California. Soil samples were taken to the laboratory, watered, and germination of seeds in the soils was determined. Fire reduced or

destroyed viability of most plant species.
Deerweed [Lotus scoparius (Nutt. in T&G.) Ottley]
and pimpernel (Anagallis arvensis L.) were the only
species with greater germination in soils from
burned areas.

Scarification by fire results in rapid
recolonization of the burned area (Rolston 1978).
One year after burning of brushlands in
southwestern Oregon more than 4,000 brush
seedlings/ha were present on burned areas compared
to 25/ha on unburned areas (Gratkowski 1961).
Brush seedlings on burned areas consisted mainly of
mountain whitethorn ceanothus (Ceanothus cordualtus
Kell.) and greenleaf manzanita (Arctostaphylos
patula Greene). Fire may crack the hard endocarp
of Arctostaphylos nuts (Berg 1974).

Fungal and Bacterial Attack

Fungi and bacteria may break down hard seed coats.
Fungal attack on the seed coats of Galium bifolium
Wats., field pennycress (Thlaspi arvense L.), and
western waterleaf [Hydrophyllum fendleri (Gray)
Heller] may increase germination (Pelton 1956).
Vest (1952) found that a fungus reduced the
hardness of shadscale [Atriplex confertifolia
(Torr.) Wats.] bracteoles, which inhibit
germination. Guttridge et al. (1984) inoculated
strawberry (Fragaria sp.) seeds with various fungi.
Ulocladium charatarum (Preuss) Simmonds,
Cladosporium sp., and the Arthrinium state of
Apiospora montagnei Sacc. promoted germination.
Stoddart and Wilkinson (1938) suggested that
microbial breakdown of the lemma and palea is
partly responsible for increasing germination of
Indian ricegrass, but Young et al. (1983) found no
evidence to substantiate this hypothesis.

Rodents

Heteromyid rodents in sandy desert rangelands of
Nevada cache Indian ricegrass seeds, a preferred
food. These rodents remove the indurate lemma,
palea and pericarp of about half of the seeds,
which enhances germination (McAdoo et al. 1983).
Merriam kangaroo rats (Dipodomys merriami Mearns)
gnaw mesquite seeds to test them for soundness when
collecting them for caches. Reynolds and
Glendening (1949) suggested that if the embryos are
undamaged, such gnawing would enhance germination.

Temperature Fluctuations

Normal soil temperature fluctuations may increase
permeability of seeds with hard coats. Martin
(1945) identified fluctuations at near freezing
temperatures as the primary factors in natural
scarification of sweet clover (Melilotus sp.)
seeds. Exposure of seeds to these conditions for 2
or more months was required for effective
scarification.

The major factor determining the rate of softening
in subterranean clover (Trifolium subterraneum L.)
and West Australian blue lupin (Lupinus varius L.)
was the maximum temperature of the fluctuation

rather than the amplitude of the fluctuation,
provided the temperature changed by at least 15° C
each day (Quinlivan 1966). In West Australian blue
lupin, temperature fluctuations caused the
strophiole to crack and allow water to enter
(Quinlivan 1968). Permeability caused by
temperature fluctuations is restricted primarily to
the strophiole in subterranean clover seeds (Hagon
1971).

ARTIFICIAL SCARIFICATION

Mechanical Scarification

Numerous methods have been used to artificially
scarify hard seeds. These methods can be grouped
into 3 general categories: (1) mechanical, (2)
chemical, and (3) hot-and-cold temperature
scarification. Mechanical scarification techniques
include (1) motorized methods, (2) abrasion by
hand, (3) nicking and pin-pricking, (4) percussion,
and (5) seed coat removal. For large amounts of
seed, physical abrasion is usually accomplished
with some type of motor-driven drum lined with
abrasive material such as sand paper or emery
cloth. Hammer mills are also used. A portion of
the seeds is usually damaged with this type of
scarification and will lose viability (Young et al.
1984). It is important to determine the optimum
length of time seeds should be treated so that
excessive treatment can be avoided. Damaged seeds
deteriorate more rapidly in storage than undamaged
seeds (Bonner et al. 1974).

Smaller lots of seed can be scarified by nicking
coats with a razor or file, rubbing seeds between 2
sheets of sandpaper or other abrasive material, or
piercing the seed coat with a sharp instrument.
Percussion or vigorous shaking increases water
absorption through the strophiole of legumes such
as white sweetclover (Melilotus alba Desr.) (Porter
1949).

Mechanical scarification may increase seedling
emergence in the field. Ansley and Abernethy
(1984) increased field emergence of Gardner
saltbush [Atriplex gardneri (Moq.) D. Dietr.]
seedlings by combining mechanical scarification
with stratification. However, field emergence was
lower than germination under laboratory conditions
because of low seedling vigor. Zemetra et al.
(1983) found that mechanical scarification
increased field emergence of Indian ricegrass.
Lower emergence in the field than under greenhouse
conditions was attributed to the land preparation
used which left the soil subject to crusting.

Mechanical scarification enhances germination by
rupturing the impermeable layer in the seed coat
and allowing water to enter (Williams and Elliott
1960). Brant et al. (1971) determined the effects
of mechanical scarification on 'Penngift'
crownvetch (Coronilla varia L.) seeds. The
treatment abraded the cuticle and penetrated the
macrosclerid cells. Hard seeds were reduced from
60 to only 4% by the treatment. Germination
enhancement from mechanical scarification may
result from factors other than physical effects on
the seed coat. Scarification of the micropylar end

of spike woodrush (_Luzula_ _spicata_ L.) seeds
stimulates germination because inhibitors are
localized at the micropyle and are removed by the
treatment (Bell and Amen 1970).

Mechanical scarification may increase the
effectiveness of other presowing treatments.
Leaching and prechilling increase germination more
in scarified than in unscarified Gardner saltbush
seeds (Ansley and Abernethy 1985). In unpublished
studies by Fulbright and Flenniken, nicking spiny
hackberry (_Celtis_ _pallida_ Torr.) seeds with a razor
blade resulted in 9% germination compared to 10%
for intact seeds. When nicked and intact seeds
were placed on substrata moistened with 100 g ml^{-1}
gibberellic acid, germination of nicked seeds (45%)
was significantly higher than that of intact seeds
(17%).

Chemical Scarification

Acids, organic solvents, enzymes, and various other
chemicals are used to scarify seeds. The chemical
most widely used in seed scarification is
concentrated sulfuric acid (H_2SO_4). Most species
that respond to mechanical scarification can be
scarified with H_2SO_4. Sulfuric acid scarification
gives results similar to nicking seed coats with a
razor for legumes such as prostrate bundleflower
[_Desmanthus_ _virgatus_ var. _depressus_ (Humbolt and
Bonpland ex Willd.) Turner] (Fulbright and
Flenniken 1987), velvet bundleflower (_Desmanthus_
velutinus Scheele.) (Haferkamp et al. 1984), and
western indigo [_Indigofera_ _miniata_ var. _leptosepala_
(Nutt.) Turner] (Kissock and Haferkamp 1983). In
studies by Brecke and Duke (1980), germination of
H_2SO_4-scarified (82%) fall panicum (_Panicum_
dichotomiflorum Michx.) seeds was similar to that
of seeds with the lemma and palea removed (85%),
while germination of the control was 0%. Brownseed
paspalum (_Paspalum_ _plicatulum_ Michx.) seeds
scarified with H_2SO_4 exhibited higher percent
germination and germination rates than seeds with
the lemma and palea removed in unpublished studies
by Fulbright and Flenniken (Table 1). In
contrast, germination of certain species that
respond to mechanical scarification may be reduced
by H_2SO_4. For example, germination of showy
menodora (_Menodora_ _longiflora_ Gray) was increased
from 53 to 81% by mechanical scarification, while
germination was inhibited by soaking in H_2SO_4
(Fulbright and Flenniken 1986).

Optimum soaking time in H_2SO_4 may vary from seconds
to 6 hours (Young et al. 1984) and may vary among
species and among strains of the same species.
Young et al. (1985) determined the effect of H_2SO_4
scarification on germination of two Indian
ricegrass varieties. 'Paloma' Indian ricegrass
seeds required 25 - 35 minutes of scarification
compared to 15 - 25 minutes for 'Nezpar' Indian
ricegrass. Variation in optimum length of soaking
among Indian ricegrass strains may result in part
from variation in the composition of polymorphic
seed forms (Young and Evans 1984, Young et al.
1985) and from variation in lemma thickness among
strains (Zemetra and Cuany 1984). Certain
precautions, in addition to determining the
optimum duration of soaking, are necessary to

Table 1. Effects of scarification, lemma and palea
removal, and gibberellic acid (GA) on
germination of brownseed paspalum seeds
from Hidalgo County, Texas at 25-35° C
(12 hours- 12 hours) under light and dark
conditions.[1]

Treatment	Percent germination[2]	Germination rate[3]	
		Light	Dark
17 M H_2SO_4 (20 min soak)	57a[4]	10a	9a
0.3 mmol liter^{-1} GA + nicking with razor	40b	7b	5b
Nick with razor	31c	5b	3c
Lemma and palea removed	26c	7b	2c
Control	6d	1c	1d

[1] From: Fulbright and Flenniken (unpublished data).
[2] Analysis for arcsine transformed percentages.
Untransformed values reported.
[3] Germination rate was calculated using the formula
of Maguire (1962).
[4] Values for percent germination are averages across
light and dark treatments. Means within a column
followed by the same letter are not significantly
different at the 0.05 level according to Tukey's
test.

prevent seed damage. It is desirable to treat
seeds in a cool water bath to prevent overheating
(Young et al. 1984). After treatment, seeds should
be rinsed in a large volume of water to remove
residual acid. Before final rinsing, seeds should
be neutralized in a solution of sodium bicarbonate
(Young et al. 1985) or some other base.

Seeds treated with H_2SO_4 may be more susceptible to
pathogens than untreated seeds. Zemetra et al.
(1983) and Stoddart and Wilkinson (1938) found that
acid scarification reduced field emergence of
Indian ricegrass. Attack by soil-borne pathogens
may have been partly responsible for reduced
emergence. Germination of acid-scarified Indian
ricegrass seeds has been improved by treatment with
maneb [ethylene bis(dithiocarbamate)] (McDonald
1976).

Sulfuric acid scarifies seeds by pitting and
dissolving the seed coat. Brant et al. (1971)
reported that H_2SO_4 treatment deeply etched the
seed coat of 'Penngift' crownvetch and dissolved
caps of the macrosclerid cells.

Effects of H_2SO_4 scarification may differ from
those of mechanical scarification because of

changes in seed biochemistry caused by the acid. Sulfuric acid scarification resulted in enhanced peroxidase, alpha-amylase, and RNase activity; delayed protein synthesis; reduced protein levels; and increased leaching of electrolytes in Indian ricegrass seeds (McDonald and Khan 1978, 1983). Tischler and Young (1983) concluded that H_2SO_4 may destroy or solubilize germination inhibitors in the seed coat of the caryopsis or in the lemma and palea of kleingrass (Panicum coloratum L.) and thus its effects are at least partially independent of scarification.

Other chemicals used to scarify seeds include sodium hypochlorite (NaOCl) and hydrogen peroxide (H_2O_2) (Frank and Larson 1970, Stidham et al. 1980, Fulbright and Flenniken 1986); absolute ethyl alcohol (Barton 1947); sodium-lye (Webster and Ratliffe 1942); citric acid (Cotrufo 1963); hydrochloric acid, pepsin, and alkaline solutions (Jelley 1937); acetone, petroleum ether, dimethyl sulfoxide, hemicellulase, and pectinase (Brant et al. 1971), and sodium hydroxide (NaOH) (Seiffert 1982). Sodium hypochlorite may partially degrade the lemma and palea of green needlegrass (Stipa viridula Trin.) (Frank and Larsen 1970). Fulbright and Flenniken (1986) compared the effects of sodium hypochlorite and mechanical scarification on germination of showy menodora. Percent germination of seeds soaked in sodium hypochlorite was similar to that of seeds nicked with a razor. Many of these chemicals may stimulate germination by physiological effects rather than by scarification, but little information is available on their mode of action.

HOT AND COLD TEMPERATURE SCARIFICATION

Hot or Boiling Water

Temperature scarification techniques include (1) hot or boiling water, (2) humid heat, (3) dry heat, and (4) freezing. Hot or boiling water is widely used to scarify legume seeds. In many cases, this treatment appears less effective than mechanical scarification or soaking seeds in H_2SO_4. Soaking prostrate bundleflower seeds in hot (80° C) water was less effective in increasing percent germination than nicking seed coats with a razor or H_2SO_4 scarification, although germination rates were similar (Table 2) (Fulbright and Flenniken 1987). Optimum levels of each treatment were determined before the comparison was made. Soaking western indigo seeds in hot (80° C) water for 3 minutes improved germination, but percent germination of hot-water-soaked seeds was less than that of seeds nicked with a razor blade or soaked in concentrated H_2SO_4 for 17 minutes (Kissock and Haferkamp 1983). Similar results have been reported for 'Penngift' crownvetch (Brant et al. 1971). Immersing mamane (Sophora chrsophylla Seem.) seeds in water at 100° C reduced germination below that of controls while germination was enhanced by H_2SO_4 and mechnical scarification (Scowcroft 1978). Lating (1961) reported similar results for Illinois bundleflower [D. illinoensis (Mich.) MacMillan].

Table 2. Effects of soaking in hot (80° C) water for 25 minutes, soaking in 17 M H_2SO_4 for 40 minutes, and nicking with a razor blade on germination of prostrate bundleflower seeds at 20-30° C (12 hours with darkness - 12 hours with light)[1].

Treatment	Percent germination	Corrected germination rate index[2]
Control	3a[3]	31a
Hot water	78b	42b
H_2SO_4	88bc	46b
Nicked	91c	41b

[1] From: Fulbright and Flenniken (1987).
[2] Corrected germination rate index was obtained by dividing the germination rate of Maguire (1962) by percent germination and multiplying by 100.
[3] Means in a column followed by the same letter are not significantly different at the 0.05 level according to Tukey's test.

Thermal scarification with water enhances germination by increasing seed coat permeability. Placing 'Penngift' crownvetch seeds in boiling water caused differential thermal expansion which separated the columnar cells of the macrosclerid layer and permitted water to enter (Brant et al. 1971). Horowitz and Taylorson (1984) suggested that possible effects of hot water soaking on legume seeds are extraction of materials impregnating the seed coat such as tannins and lipids and disruption of structural elements responsible for impermeability. Treating seeds in boiling water may also cause thermal shock to the embryo or leaching of soluble inhibitors (Young et al. 1984).

Subjecting seeds to warm temperatures and high humidity increases seed coat permeability in certain species. Humid heat (68° C) for 1 hour reduced hard seeds in velvetleaf (Abutilon theophrasti Medic.) by 50% (Horowitz and Taylorson 1984). However, immersion in hot water increased germination more effectively than humid heat.

Many species naturally scarified by fire respond to dry heat treatments (Gratkowski 1961) in which unimbibed seeds are exposed to high temperatures in ovens. Effective temperatures range from 40 to 130° C and effective duration of treatment ranges from minutes to weeks. Dry heat was less effective in increasing germination of velvetleaf than immersing seeds in hot water (Horowitz and Taylorson 1984). Martin et al. (1975) determined the effects of 4-minute exposures to humid and dry heat on germination of seeds of 18 legume species from the southeastern United States. Humid heat increased germination of 8 species and dry heat increased germination of 7 species. Maximum germination generally occurred with 70° C humid heat treatments and 90° C dry heat treatments. Dry

heat (70° C) for 24 hours was as effective as mechanical scarification in a Forsberg seed cleaner for increasing germination of Lehmann lovegrass (Eragrostis lehmanniana Nees.) seeds (Haferkamp and Jordan 1977).

Dry heat treatments may enhance germination through rupture of the seed coat or possibly through physiological effects or a combination of both. Dry heat may disrupt the gelatinous coating which covers Lehmann lovegrass seeds and can be a barrier to water and gas when moistened (Haferkamp and Jordan 1977). Dry heat at certain stages of physiological development may cause reorganization of some structural compounds and/or denaturization of others. In indigobush amorpha (Amorpha fruticosa L.) seeds, dry heat caused localized fissures in the hilum region and allowed water entry (Hutton and Porter 1937).

Various low temperature treatments have been used to increase germination of seeds with hard coats. In 'Penngift' crownvetch seeds, a 1-minute dip in liquid nitrogen increased germination (Brant et al. 1971). Apparently, dipping seeds in liquid nitrogen resulted in differential thermal expansion which separated the columnar cells of the macrosclerid layer and permitted water to enter. Busse (1930) reported that cooling to -80° C increased the number of permeable alfalfa (Medicago sativa L.) seeds.

FACTORS AFFECTING THE PERCENTAGE OF HARD SEEDS

The percentage of hard seeds may vary between species or between ecotypes, varieties, or cultivars of a species because of genetic differences. For example, Indian ricegrass varieties may vary in duration of H_2SO_4 scarification necessary to produce maximum germination because of differences in the composition of polymorphic seed forms (Young and Evans 1984, Young et al. 1985) and lemma thickness. In studies by Zemetra and Cuany (1984), lemma thickness of this species varied among strains but not between seed harvest locations.

Nongenetic factors may cause the composition of hard seeds to vary for the same species between years or between locations where seeds are produced. These factors include (1) seed age, (2) stage of maturity when harvested, (3) seed moisture content, and (4) environmental conditions at the time of harvest. Seed coat impermeability of Illinois bundleflower increased with length of storage from 1 to 4 years, while impermeability of western indigo decreased (Call 1985). Germinating green needlegrass seeds in an oxygen-enriched environment more effectively relieved lemma-and-palea-imposed dormancy as seeds aged (Frank and Larson 1970). The lemma and palea became more permeable or less of a mechanical restriction with age. Raising of a "blister" formed by separation of the pallisade layer of the seed coat from underlying tissues preceded water uptake by prickly sida (Sida spinosa L.) seeds (Egley and Paul 1982). In afterripened (nonhard) seeds the palisade separated from the subpalisade

upon wetting, but in nonafterripened (hard) seeds wetting did not result in separation.

Percentage of hard seeds may be influenced by stage of maturity. Brown (1955) reported that impermeable seed content of birdsfoot trefoil (Lotus corniculatus L.) increased with increasing maturity. Delaying harvest up to 6 weeks after the normal stage of maturity caused a reduction in the percentage of hard seeds in subterranean clover (Trifolium subterraneum L.) (Loftus Hills 1942).

Seeds with a high moisture content may be more permeable than those with a low moisture content. High soil moisture availability during seedfill reduced the percentage of impermeable seeds in soybean (Glycine max L.) by disrupting seed coat integrity (Hill et al. 1986). Cotyledon expansion was greater in seeds from well-watered plants and pressure of the cotyledons on the seed coat caused it to weaken or rupture. In subterranean clover, as seeds dried on the plant the percentage of impermeable seeds increased (Aitken 1939). Hard seed formation may also be associated with dehydration processes that occur independently of the plant (Williams and Elliott 1960).

Environmental factors such as temperature, relative humidity, light, and soil fertility may affect hard seed content. Percentage of hard seeds in alfalfa tends to be lower in seeds from lower altitudes than in seeds from higher altitudes (Dexter 1955). Soybeans growing in sites with low relative humidity and high temperatures develop more hard seeds than those in sites with higher relative humdity and lower temperatures (Rolston 1978). Gutterman and Heydecker (1973) found that reduced day length during the last 8 days of ripening decreased the hard seed content of Ononis sicula Guss.

Soil fertility plays a minor role in the development of impermeable seeds (Rolston 1978). A combination of potassium sulfate (476 kg ha^{-1}) and ammonium sulfate (476 kg ha^{-1}) decreased the impermeable seed content of Egyptian clover (Trifolium alexandrium L.) (el Bagoury and Niyazi 1973). In contrast, potassium sulfate (238 kg ha^{-1}) increased the hard seed content of broad bean (Vicia faba L.) from 10 to 20% (el Bagoury 1975).

CONCLUSIONS AND RESEARCH NEEDS

For certain plant species, germination enhancement of seeds with hard coats by artificial scarification may result in part or totally from physiological effects rather than from physical effects on the seed coat. Why certain treatments enhance germination of certain species is unknown. For example, H_2O_2 stimulates germination of antelope bitterbrush [Purshia tridentata (Pursh) DC.], desert bitterbrush (P. glandulosa Curran.), and cliff rose [Cowania mexicana var. stansburiana (Torr.) Jeps] but the reason is unknown (Young and Evans 1981). According to Young and Evans (1981), if the nature of germination enhancement from H_2O_2 treatments was understood, it might be possible to perfect the methodology to increase germination enhancement of these species. Understanding the

nature of enhancement would enable researchers to perfect the methodology for enhancing germination of numerous other species.

Seed-coat-imposed dormancy and physiological dormancy appear to interact for species such as Gardner saltbush. For such species, combinations of scarification and physiological treatments are necessary for maximum germination enhancement. More research is needed to determine the nature of these interactions, e.g., to determine why physiological treatments may work better for scarified seeds than unscarified seeds.

In hard-coated seeds of certain species, structural changes in the seed coat may occur during afterripening that decrease the percentage of hard seeds. In contrast, seed coat permeability decreases as seeds age in certain species. Research to determine the changes that occur in seed coat structure during storage and the interrelationships between physiological changes and changes in seed coats during afterripening is needed.

Treatments that increase germination of 1 lot of a species may not be effective on or may even inhibit germination of a different lot because of differences in hard seed content. The optimum level of treatment for each lot should be determined to avoid under or over treating seeds.

There is a paucity of research concerning the effects of natural and artificial scarification on germination and seedling emergence in the field. Greater knowledge of the role of natural scarification in facilitating plant establishment and the spread of undesirable species would aid in developing range management practices to promote establishment of desirable species and inhibit establishment of undesirable plants. More information concerning effects of scarification on seedling vigor and establishment, attack of seeds and seedlings by soil-borne pathogens, and on planting methods for treated seeds would aid in developing more effective techniques of artificially seeding rangelands.

LITERATURE CITED

Aitken, Yvonne. 1939. The problem of hard seeds in subterranean clover. Proc. Roy. Soc. Victoria 51:187-213.

Amen, R. D. 1966. The extent and role of dormancy in alpine plants. Quart. Rev. Bio. 41:271-281.

Ansley, J. A., and R. H. Abernethy. 1984. Seed pretreatments and their effects on field establishment of spring-seeded Gardner saltbush. J. Range Manage. 37:509-513.

Ansley, J. A., and R. H. Abernethy. 1985. Environmental factors influencing Gardner saltbush seed dormancy alleviation. J. Range Manage. 38:331-335.

Barton, L. V. 1947. Special studies on seed coat impermeability. Cont. Boyce Thompson Inst. 14:335-362.

Bell, K. L., and R. D. Amen. 1970. Seed dormancy in Luzula spicata and L. parviflora. Ecology 51:492-496.

Berg, A. R. 1974. Arctostaphylos Adans. Manzanita. Pp. 228-231 in C. S. Schopmeyer, technical coordinator, Seeds of woody plants in the United States. Agr. Handbook No. 450. USDA, For. Serv., Washington, D. C. 883 p.

Beweley, J. D., and M. Black. 1982. Physiology and biochemistry of seeds in relation to germination, vol. 2. Springer-Verlag, Berlin. 375 p.

Bonner, F. T., B. F. Mclemore, and J. P. Barnett. 1974. Presowing treatment of seed to speed germination. Pp. 126-135 in C. S. Schopmeyer, technical coordinator, Seeds of woody plants in the United States. Agr. Handbook No. 450. USDA, For. Serv., Washington, D. C. 883 p.

Brant, R. E., G. W. McKee, and R. W. Cleveland. 1971. Effect of chemical and physical treatment on hard seed of Penngift crownvetch. Crop Sci. 11:1-6.

Brecke, B. J., and W. B. Duke. 1980. Dormancy, germination, and emergence characteristics of fall panicum (Panicum dichotomiflorum) seed. Weed Sci. 28:683-685.

Brown, C. S. 1955. Hard seed in birdsfoot trefoil. Unpublished Ph. D. Dissertation, Cornell University.

Busse, W. F. 1930. Effect of low temperatures on the germination of seed. Bot. Gaz. (Crawfordsville) 89:169-179.

Call, C. A. 1985. Storage life of Illinois bundleflower and western indigo seed. J. Range Manage. 38:500-503.

Cotrufo, C. 1963. Stimulation by citric acid of germination of eastern red cedar (Juniperus virginiana L.). Nature 199:92-93.

Dexter, S. T. 1955. Alfalfa seedling emergence from seed lots varying in origin and hard seed content. Agron. J. 47:357-361.

Egley, G. H., and R. N. Paul, Jr. 1982. Development, structure and function of subpalisade cells in water impermeable Sida spinosa seeds. Amer. J. Bot. 69:1402-1409.

el Bagoury, O. H. 1975. Effect of different fertilizers on the germination and hard seed percentage of broad bean seeds (Vicia faba). Seed Sci. and Tech. 3:569-574.

el Bagoury, O. H., and M. A. Niyazi. 1973. Effect of different fertilizers on the germination and hard seed percentages of Egyptian clover seeds (Trifolium alexandrinum L.). Seed Sci. and Tech. 1:773-779.

Fisher, C. E., C. H. Meadors, R. Behrens, E. D. Robinson, P. T. Marion, and H. T. Morton. 1959. Control of mesquite on grazing lands. Tex. Agr. Exp. Sta. Bulletin 935. College Sta., Tex. 24 p.

Frank, A. B., and K. L. Larson. 1970. Influence of oxygen, sodium hypochlorite, and dehulling on germination of green needlegrass seed (Stipa viridula Trin.). Crop Sci. 10:679-682.

Fulbright, T. E., and K. S. Flenniken. 1986. Effects of temperature and presowing treatments on showy menodora seed germination. J. Range Manage. 39:310-313.

Fulbright, T. E., and K. S. Flenniken. 1987. Temperature and scarification effects on germination of prostrate bundleflower. J. Range Manage. 40:170-173.

Gratkowski, H. 1961. Brush seedlings after controlled burning of brushlands in southwestern Oregon. J. For. 59:885-888.

Gutterman, Y., and W. Heydecker. 1973. Studies of the surfaces of desert plant seeds. I. Effect of daylength upon maturation of the seedcoat of Ononis sicula Guss. Ann. Bot. (London) 37:1049-1050.

Guttridge, C. G, S. E. Woodley, and T. Hunter. 1984. Accelerating strawberry seed germination by fungal infection. Annals of Bot. 54:223-230.

Haferkamp, M. R., and G. L. Jordan. 1977. The effect of selected presowing treatments on germination of Lehmann lovegrass seeds. J. Range Manage. 30:151-153.

Haferkamp, M. R., D. C. Kissock, and R. D. Webster. 1984. Impact of presowing seed treatments, temperature and seed coats on germination of velvet bundleflower. J. Range Manage. 37:185-188.

Hagon, M. W. 1971. The action of temperature fluctuations on hard seeds of subterranean clover. Aust. J. Exp. Anim. Husb. 11:440-443.

Hill, H. J., S. H. West, and K. Hinson. 1986. Effect of water stress during seedfill on impermeable seed expression in soybean. Crop Sci. 26:807-812.

Horowitz, M., and R. B. Taylorson. 1984. Hardseededness and germinability of velvetleaf (Abutilon theophrasti) as affected by temperature and moisture. Weed Sci. 32:111-115.

Hutton, M. E. J., and R. H. Porter. 1937. Seed impermeability and viability of native and introduced species of Leguminosae. Iowa State Coll. J. Sci. 15:5-24.

Kissock, D. C., and M. R. Haferkamp. 1983. Presowing seed treatment and temperature effects on germination of Engelmannia pinnatifida and Indigofera miniata var. leptosepala. J. Range Manage. 36:94-97.

Jelley, M. E. 1937. Eastern red cedar. J. For. 35:865-867.

Lating, J. 1961. The biology of Desmanthus illinoensis. Ecology 42:487-493.

Lieberman, D., J. B. Hall, and M. D. Swaine. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. Ecology 60:65-75.

Loftus Hills, K. 1942. Dormancy and hardseededness in T. subterraneum. 1. The effect of time of harvest and of certain seed storage conditions. J. Aust. Coun. Sci. Ind. Res. 15:275-284.

Maguire, J. D. 1962. Speed of germination- aid in selection and evaluation for seedling emergence and vigor. Crop Sci. 2:176-177.

Martin, J. N. 1945. Germination studies of sweet clover seed. Iowa St. Coll. J. Sci. 19:289-300.

Martin, R. E., R. L. Miller, and C. T. Cushwa. 1975. Germination response of legume seeds subjected to moist and dry heat. Ecology 56:1441-1445.

McAdoo, J. K., C. C. Evans, B. A. Roundy, J. A. Young, and R. A. Evans. 1983. Influence of heteromyid rodents on Oryzopsis hymenoides germination. J. Range Manage. 36:61-64.

McCully, W. G. 1951. Recovery and viability of Macartney rose seeds fed to cattle. J. Range Manage. 4:101-106.

McDonald, M. B., Jr. 1976. Improving the germination of Indian ricegrass seeds. J. Seed Tech. 1:44-53.

McDonald, M. B., Jr., and A. A. Khan. 1978. Metabolic changes in Indian ricegrass seeds in relation to coat-imposed and embryonal dormancy. Agron. J. 70:829-835.

McDonald, M. B., Jr., and A. A. Khan. 1983. Acid scarification and protein synthesis during seed germination. Agron. J. 75:111-114.

Pelton, J. 1956. A study of seed dormancy in eighteen species of high altitude Colorado plants. Butler Univ. Bot. Stud. 13:74-84.

Porter, R. H. 1949. Recent developments in seed technology. Bot. Rev. 15:221-344.

Potter, R. L., J. L. Petersen, and D. N. Ueckert. 1984. Germination responses of Opuntia spp. to temperature, scarification, and other seed treatments. Weed Sci. 32:106-110.

Quinlivan, B. J. 1966. The relationship between temperature fluctuations and the softening of hard seeds of some legume species. Aust. J. Agr. Res. 12:1009-1022.

Quinlivan, B. J. 1968. The softening of hard seeds of sand-plain lupin (Lupinus varius L.). Aust. J. Agr. Res. 19:507-515.

Reynolds, H. G., and G. E. Glendening. 1949. Merriam kangaroo rat, a factor in mesquite propagation on southern Arizona rangelands. J. Range Manage. 2:193-197.

Rolston, M. P. 1978. Water impermeable seed dormancy. Bot. Rev. 44:365-396.

Scifres, C. J., J. L. Mutz, and D. L. Drawe. 1982. Ecology and management of huisache on the Texas Coastal Prairie. Tex. A&M Univ., Tex. Agr. Exp. Sta. B-1408. College Sta., Tex. 21 p.

Scowcroft, P. G. 1978. Germination of Sophora chrysophylla increased by presowing treatment. Res. Note PSW-327. Pacific Southwest Forest and Range Experiment Station, Forest Serv., USDA, Berkeley, Calif.

Seiffert, N. F. 1982. Practical method for Leucaena seed scarification using NaOH. Council for Agricultural Planning and Development, Taipei, Taiwan, Leucaena Research Reports 4:5-6.

Stidham, N. D., R. M. Ahring, J. Powell, and P. L. Claypool. 1980. Chemical scarification, moist prechilling, and thiourea effects on germination of 18 shrub species. J. Range Manage. 33:115-118.

Stoddart, L. A., and K. L. Wilkinson. 1938. Inducing germination in Oryzopsis hymenoides for range seeding. J. Am. Soc. Agron. 30:763-768.

Stone, E. C., and G. Juhren. 1951. The effect of fire on the germination of the seed of Rhus ovata Wats. Amer. J. Bot. 38:368-372.

Tischler, C. R., and B. A. Young. 1983. Effects of chemical and physical treatments on germination of freshly harvested kleingrass seed. Crop Sci. 23:789-792.

Vest, E. D. 1952. A preliminary study of some of the germination characteristics of Atriplex confertifolia. Unpublished master's thesis, University of Utah, Salt Lake City.

Webster, C. B., and G. T. Ratliffe. 1942. A method of forcing quick germination of Juniperus virginiana seed. J. For. 40:268.

Went, F. W., G. Juhren, and M. C. Juhren. 1952. Fire and biotic factors affecting germination. Ecology 33:351-364.

Williams, W. A., and J. R. Elliott. 1960. Ecological significance of seed coat impermeability to moisture in crimson, subterreanean and rose clovers in a Mediterranean-type climate. Ecology 41:733-742.

Young, J. A., and R. A. Evans. 1981. Germination of seeds of antelope bitterbrush, desert bitterbrush, and cliff rose. USDA-SEA Agricultural Research Results. ARS-W-17. USDA-SEA, Oakland, Calif.

Young, J. A., and R. A. Evans. 1984. Germination of seeds of 'Paloma' and 'Nezpar' Indian ricegrass. J. Range Manage. 37:19-21.

Young, J. A., R. A. Evans, and D. A. Easi. 1985. Enhancing germination of Indian ricegrass seeds with sulfuric acid. Agron. J. 77:203-206.

Young, J. A., R. A. Evans, and B. A. Roundy. 1983. Quantity and germinability of Oryzopsis hymenoides seed in Lahontan sands. J. Range Manage. 36:82-86.

Young, J. A., J. D. Budy, and R. A. Evans. 1984. Germination of seeds of wildland plants. Pp. 1-5 in P. M. Murphy, compiler, The challenge of producing native plants for the Intermountain area. Proc. Intermountain Nurseryman's Association 1983 Conference. General Tech. Rep. INT-168, Ogden, Utah. USDA For. Ser., Intermountain For. and Range Exp. Sta. 96 p.

Zemetra, R. S., and R. L. Cuany. 1984. Variation in lemma thickness in Indian ricegrass: Implications for dormancy, scarification, and breeding. Crop Sci. 24:1082-1084.

Zemetra, R. S., C. Havstad, and R. L. Cuany. 1983. Reducing seed dormancy in Indian ricegrass (Oryzopsis hymenoides). J. Range Manage. 36:239-241.

NATIONAL AND INTERNATIONAL SIGNIFICANCE OF
SEED AND SEEDBED ECOLOGY OF RANGELAND PLANTS

Robert F. Barnes[1]

ABSTRACT

Plant germplasm has become increasingly
important in raising farm productivity.
Concern has been expressed over future
sources and availability of genetic and
biological diversity. Global reaction has
highlighted the significance of genetic
resources in agricultural science and
production. National policy toward the
stewardship of resources and the environment
are discussed.

INTRODUCTION

Agriculture has been properly described as
the basic human enterprise. It involves the
fundamental processes of sustaining life
through an adequate supply of wholesome food
and fiber. Today, as we examine the
significance of seed and seedbed ecology of
rangeland plants, let us not forget that
agriculture must be understood as a complex
set of technical, ecological, economic,
social, and political interactions involving
the seeding, producing, harvesting, storing,
processing, marketing, and consuming of a
variety of renewable natural resources on a
worldwide basis.

First--The Seed

I understand that the motto of the American
Seed Trade Association is, "First--The Seed".
There is much truth to that simple statement,
and recently there has been increasing
attention given to "seed". The demand for
legume and grass seed is predicted to
increase, largely based on the need for
forage and rangeland seedings to provide
for:

   Conservation reserve 'set-aside'
   acreages

   Forage cover crops

   Increased productivity of soils in
   rotational cropping systems

   Increased marketing of "grass-fed"
   livestock

   Clean air and water

[1]Executive Vice President, American
Society of Agronomy-Crop Science Society
of America-Soil Science Society of
America, 677 South Segoe Road, Madison,
WI 53711.

Control of nonpoint pollution

   Increased cost for nitrogen for
   production of competing crops

In fact, "seeds of controversy" has become a
coined phrase in many articles and speeches
(Shulman 1986). Why is there this sudden
"seedbed" of debate and contention over a
topic that has often been taken for granted
and for which limited attention has been
given in the past?

Plant germplasm, which refers to the genetic
information encoded in seed, is fundamental
to crop and rangeland establishment, growth,
development, production, and profitability.
Plant genetic resources are the raw materials
of the plant breeder, the genetic engineer,
and the biotechnologist. It has been said
that genetic wealth, especially in tropical
areas such as rain forests, until now a
relatively inaccessible trust fund, is
becoming a currency of high immediate value.
A recent report of the Council for
Agricultural Science and Technology (Otto et
al. 1985) states that valuable genetic
sources of breeding materials for crop
improvement are being irretrievably lost in
the U.S. and developing countries.

At the recent AAAS meetings in Chicago, Avery
(1987) stated that plant genetics have become
the foremost factor in the rise of world farm
productivity in recent years. Better seeds
are relatively cheap, both to develop and
use. Even primitive farmers can adopt
breakthrough seed cultivars rather rapidly.
Third World governments are implementing
reforms to help their farmers cut production
costs and increase output. They are aided
enormously by the fact that recent technology
advances--especially better plant
genetics--are helping low-tech farms even
more than high-tech farmers. It appears that
the technological pendulum is swinging toward
the lower-tech farms.

Plant Breeders' Rights

The seed industry became international in the
1970's. In the United States, sexually
reproduced crop cultivars were provided some
protection in 1970, with the passage of the
Plant Variety Protection Act (PVPA as amended
in 1980) (Otto et al. 1985). The PVPA
protects the breeder of a new, stable, and
uniform variety from a seedsman who might
want to reproduce the cultivar for sale.
Private companies reached out for global
markets and sought global extension of a
legal framework that would give them
proprietary rights to the new seed cultivars
they were developing. Controversy over the
institution of plant breeders' rights, in
both developed and developing nations,
necessarily entailed consideration of the
commerical value of the elite forms of plant
germplasm. The question was asked, "Is the

germplasm of one country's wild varieties of major food crops a global resource, as some say, to be shared and exchanged freely? Or, as others contend, is it a natural resource more akin to ores like iron, a saleable asset for the country possessing it, even in its "unrefined state"? (Shulman 1986). Plant genetic resources are increasingly seen as a valuable, even vital, strategic raw material for world agriculture. The establishment of some framework for compensation of access to plant genetic resources has been suggested as a necessry step in resolving the germplasm controversy (Kloppenburg and Kleinman 1987).

Plant variety rights (plant breeders' rights) is one of the most contentious issues associated with plant genetic resources. Two factions are involved, one of which states that genes are a common world heritage and in the public domain and, therefore, cannot be patented. They contend that patents trigger secrecy and may hinder the flow of germplasm, further reducing genetic and biological diversity due to the interest of the breeders' desire for crop uniformity. Others contend that only when patents or royalties are available on the finished product is there sufficient stimulus for research and devlopment in agriculture, or any other scientific enterprise.

Approximately 20 countries have enacted plant variety rights (Plunknett et al. 1987). However, it should also be pointed out that farmers are free to reproduce seed for their own uses and may even sell limited amounts of seed. Also, there are no restrictions applied for research use of cultivars covered by the PVPA.

All countries depend on plant germplasm, but the vagaries of natural history have distributed plant genetic resources unequally. In this debate, the so-called "gene-poor" developed countries that depend on the diversity found in the world's germplasm for breeding elite hybrid crop cultivars are pitted against the "gene-rich" primarily developing countries, home to the vast majority of the remaining genetic base for most of the world's major crops.

In 1981, the Third World countries lead by Libya, Mexico, and Peru, proposed that the gene bank networks be under the jurisdiction of the Foreign Agricultural Organization (FAO) of the United Nations (Plucknett et al. 1987). Under FAO an International Commission on Plant Genetic Resources was established to oversee the launching of a legally nonbinding international undertaking on plant genetic resouces. The undertaking established principles on collection, maintenance, and exchange. It included elite and current breeders lines, as well as special genetic stocks.

The proposal was opposed by countries recognizing plant variety rights. They contended that gene banks should emphasize primitive varieties (that is, landraces), wild relatives, and obsolete cultivars. The Wall Street Journal (Paul 1984) called this international controversy "seed wars" that could have serious repercussions for both agricultural science and production.

In 1985, a decision of the U.S. Board of Patent Appeals (1985) ruled in Ex parte Hibberd, that Section 101 of the U.S. Patent Act does apply to seeds, plants, plant parts, and tissue cultures, thus, allowing biogenetically engineered plants, seeds, and tissue cultures to be patended. The criteria required "novelty, non-obviousness, and utility", rather than criteria under the Plant Variety Protection Act of "novelty, uniformity, and stability". The Board of Patent Appeals Act decision has paved the way for commercializing agricultural biotechnology. However, it has been contended that patenting genetic materials entails material with many problems, analogous to patenting computer software, that is, the value resides in the encoded information, which is easily reproduced.

Plant Genetic Resources

The controversy over global plant genetic resources has lead to the establishment of the Committee on Genetic Resources by the National Academy of Sciences, National Research Council Board on Agriculture (Diversity 1986 c). Dr. John A. Pino will head the committee and oversee a three-year study on managing global genetic resources. The committee will address the following issues:

> Techniques, methods, and strategies for germplasm collection, assessment, and preservation.
>
> Control over access to germplasm, including economic and geopolitical issues.
>
> The scope of U.S. and non-U.S. efforts in collection and management of germplasm.
>
> The performance of the U.S. germplasm system.

Pino's committee is expected to enhance the scientific community by assessing the situation and enlightening scientists on public perceptions and policies on the ability to freely exchange germplasm; and by involving scientists in the committee's activities, through the analysis of food capability and proposals to change the legal, institutional, economic, and administrative foundation of existing germplasm systems.

The U.S. Congress, Office of Technology Assessment (1987) is publishing a report on "Technologies to Maintain Biological Diversity". The report commends the National Plant Germplasm System (NPGS) as the "best-defined" of all U.S. federal policies and programs responsible for maintaining germplasm diversity. However, it has made minimal effort to either recognize grassroot activities or incorporate their materials into the national system. The report also speaks of grassroot groups with local focus and flexibility, which are vulnerable, due to limited or unstable funding, and dependence on the enthusiasm of a single individual or small group.

The OTA grassroots report identified two gaps in the National Plant Germplasm System, as the lack of attention to traditional varieties, and the lack of attention to varieties no longer available from commercial sources. It was reported in Diversity (1985 b), that the Board on Agriculture perceives "a growing gap in public understanding of the critical role germplasm plays in feeding the world". In establishing the Committee on Global Resources, the Board wants to assure that public policy on this issue is developed in accordance with the best understanding of the scientific potential that exists in this area.

Activist Jeremie Rifkin, of the Foundation on Economic Trends, lead a coalition of national and international organizations to sue the U.S. Department of Agriculture, charging the Government with gross negligence in its national Germplasm Program and its consequent failure to protect vital germplasm resources entrusted to it from countries around the world (Diversity 1986 a). A recent environmental assessment was prepared by the U.S. Department of Agriculture, Agricultural Research Service and published in Diversity (1987 b). Rifkin and his co-plaintiffs, however, have rejected that statement and it now appears that a full Environmental Impact Statement on the USDA's germplasm program will be requested (Diversity 1987 a). Deborah Strauss, Editor of Diversity, recently summed it up with the statement, "Court actions, legislative proposals, and regulatory decisions have occurred that now draw all three branches of our national Government directly into the debate over plant genetic resources. Developments on the international scene have also intensified, as the global germplasm system comes under increasing scrutiny" (Shulman 1986).

Agriculture today is dependent upon an international economy. There is a growing importance of the Third World, that is, developing countries, as we have discussed, relative to the importance of plant genetic resources.

In dealing with an international economy, we must understand our changing comparative advantage and competitive position in such an economy. We need to understand fully the agriculture of other countries, their soils, plants, and animals; and their abilities to respond to changing economic conditions and the production technology they use. We need to tap into new knowledge being generated elsewhere, through expanded programs of translation, the identification of bilingual scientists and administrators, and the establishment of collaborative relationships between U.S. and foreign institutions, including more exchanges of researchers.

Conservation Issues

Some of the challenges and constraints, relating to the significance of seedbed ecology, include:

> The natural resource base is declining in quantity and quality,
>
> Groundwater supplies are diminishing,
>
> Half the original topsoil has been removed by erosion, and excessive erosion occurs on approximately one-third of the nation's farmland,
>
> Salinization of land and water is occurring,
>
> There is increasing regulation of agricultural chemicals and processes,
>
> Actual or potential environmental constraints are increasing, such as air pollution, reduced water quality, and acid rain, and
>
> The loss of potentially valuable plant genetic resources is threatened.

The commodity policies designed in the 1930's to encourage full production every year, are now a barrier to adjustment within agriculture. Agricultural policy is now seen as a crucial arena, with both national and international significance. With passage of the 1985 Farm Bill, the Food Security Act, an attempt was made to achieve agricultural commodity and conservation objectives through a single program (Benbrook 1986). The basic goals of the new conservation policy are:

1. To get fragile lands, already in production, into a stable forage or forestry based land use.

2. To implement the sodbuster and swampbuster provisions, which are designed to provide strong penalties for plowing up, or draining, agricultural lands that have severe resource-based limitations.

A further important policy in the new Farm
Bill is conservation compliance. By 1990,
all producers are required to begin
controlling erosion on all highly-erodible
land now in production, with full compliance
by 1995--or be subject to the
sodbuster/swampbuster provisions. To fully
meet the standard called for in conservation
compliance, a farmer will need to be applying
an approved conservation plan that
effectively brings erosion down to, or near,
pertinent T values. However, there are some
scientists that question the effectiveness of
the current calculations to measure T values
and further research will likely be needed to
clarify the matter.

Many of you are all too familiar with the
impact of the CRP upon available supplies of
seed stocks for use in the program. Gearing
up to produce adequate seed stocks of
desirable quality will be a challenge in the
near future and one in which careful
assessment of needs and recommended
species/ecotypes should be taken into
consideration.

Concluding Statement

The 1985 Farm Bill moved U.S. agricultural
policy closer to the principle of stewardship
of resources and the environment. It is
imperative that a strong research and
educational program be initiated, that is
complimentary to such conservation policy
issues, and in fact, leads the way toward
their implementation. "Today we must meet
the new challenges of ecology, of increased
scientific knowledge, of changing world
societies, and of the simple economic facts
of life in agriculture. Social responsiility
has been added to the criteria by which our
accomplishments are judged" (Duvick 1986).

Yes, there are many factors of national and
international significance related to seed
and seedbed ecology of rangeland plants.
Yet, on the positive side, it should be
recognized that we have many resources to
draw upon in facing these questions and
dilemmas. Hopefully, the industrial
societies will be able to learn and practice
the wisdom of the millenia of peasants and
farmers, that is, that in addition to finding
ways to get along with one's neighbors, the
ultimate sources of security lie in
conserving one's fields, animals, and
especially each year's heritage of
regeneration--the seed (Dahlberg 1987).

LITERATURE CITED

Avery, Dennis T. 1987. Global farm
    competition: strange, stunted--but
    beautiful. American Association for the
    Advancement of Science Abstracts, Chicago,
    Ill.

Benbrook, Charles M. 1986. A perspective
    on conservation policy challenges and
    opportunities. Speech presented at
    annual summer school meeting of the Ohio
    Federation of Soil and Water Conservation
    Districts, July 28, 1986.

Dahlberg, Kenneth A. 1987. Redefining
    development priorities: genetic
    diversity and agrodevelopment.
    American Association for the Advancement
    of Science Abstracts, Chicago, Ill.

Diversity. 1986 a. Rifkin sues USDA. No.
    8, p. 4-5.

Diversity. 1986 b. National academy to
    study germplasm. No. 8, p. 6-7.

Diversity. 1986 c. Pino to lead global
    germplasm study. No. 9, p. 4.

Diversity. 1987 a. USDA releases
    environmental assessment of germplasm
    program: "no significant impact".
    No. 10, p. 4.

Diversity. 1987 b. Environmental
    assessment USDA germplasm program.
    No. 10, p. 4.

Duvick, Donald N. 1986. The nobility
    of seed research and its critics. The
    World & I: A Chronicle of Our
    Changing Era, Reprint No. 860701,
    No. 7, p. 275.

Klopenburg, Jack, Jr. and Daniel Lee
    Kleinman. 1987. The plant germplasm
    controversy. BioScience 37:190-198.

Otto, H. J. ed. 1985. Plant germplasm
    preservation and utilization in U.S.
    agriculture. Council for Agricultural
    Science nd Technology Report No. 106.

Paul, B. 1984. Third world battles for
    fruit of its seed stocks. The Wall
    Street Journal. June 15:1.

Plunkett, Donald L., Nigel J.H. Smith,
    J.T. Williams, and N. Murthi Anishetty.
    1987. Gene banks and the world's food.
    Princeton University Press, Princeton,
    N.J.

Shulman, Seth. 1986. Seeds of controversy.
    BioScience 36:647-651.

U.S. Board of Patent Appeals and
    Interferences. 1985. Ex parte Kenneth
    Hibbert et al. 18 Septemer. Washington,
    D.C.

U.S. Congress, Office of Technology
    Assessment (OTA). 1987. Technologies
    to maintain biological diversity. OTA.
    Washington, D.C.

SEEDBED MODIFICATION WITH WEED CONTROL AND SEEDING

Raymond A. Evans and James A. Young[1]

ABSTRACT

Control of both woody and herbaceous species is important for establishment of seeded species on sagebrush/grass rangelands of the Intermountain West. Control of cheatgrass (Bromus tectorum L.) is critical in many areas for establishment of perennial forage species. Mechanical and herbicidal methods for control of cheatgrass have been developed.

INTRODUCTION

The attitude of range managers toward methods of weed control to enhance the establishment of seeded forage or browse species has undergone a near complete reversal during the last two decades. After World War II and during the early 1950's, range improvement through weed control and seeding was very active on the western range, especially in the sagebrush/grass ranges of the Intermountain area. The seeding of crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Schult.] was very popular. Hundreds of thousands of hectares of rangeland were seeded with crested wheatgrass for the biological suppression of halogeton [Halogeton glomeratus (Bieb.) C.A. Mey.] with funds supplied by the federal government and much of the seeding carried out on publically owned rangeland.

The livestock industry in Nevada illustrates the impact of this perennial grass seeding program. The state contains 11.6 million hectares of big sagebrush/grass rangeland. About 400,000 ha (3.4 percent) were seeded to crested wheatgrass from 1944 through 1960. It is estimated that the seeded area supports or supplies 20 percent of the forage base for the range livestock industry in Nevada.

CRESTED WHEATGRASS SEEDING

The wholesale seeding of sagebrush rangelands had biological, political and economic consequences through the Intermountain area. Biologically, the conversion from degraded big sagebush (Artemisia tridentata Nutt.) back to perennial grass dominance reversed a long downward trend in range condition. The full ecological ramifications of large-scale seeding of crested wheatgrass would require a volume by itself (Young and Evans 1986). Politically, the established crested wheatgrass seedings on an allotment were a powerful bargaining tool for the land management

---

[1] Range scientist, retired, and Range scientist, U.S. Dept. of Agric., Agric. Res. Ser., 920 Valley Road, Reno, NV 89512.

agencies in the development of rudimentary management on public rangelands. Economically, crested wheatgrass provided an alternative to the continued reduction in the number of animals permitted on public lands and most ranchers gained in management flexibility with the addition of crested wheatgrass seeding. In the Vale District of National Resource Lands (Oregon) administered by the Bureau of Land Management, U.S. Dept. of Interior, a most striking example of environmental change of crested wheatgrass seeding became apparent when the results of large-scale range improvement in the district were examined by independent range scientists. Seeding of crested wheatgrass resulted in a significant improvement in range condition in the Vale District compared to the majority of districts that consisted of unimproved native rangeland (Heady and Bartolome 1977).

The establishment of crested wheatgrass in the Intermountain area was initially conducted on abandoned cropland. This was mainly cereal grain-fallow land that had proven to be too drought prone for consistent production. Standard farm tools for tillage and seeding were used to convert these areas to perennial grass (Young and Evans 1986).

Big sagebrush stands provided a much more difficult conversion problem for the establishment of crested wheatgrass. The woody big sagebrush plants left a trashy, uneven seedbed which, coupled with rocks and uneven topography, made it difficult to seed with conventional grain drills (Young and McKenzie 1982). The use of the brushland plow aggravated this problem by creating a very rough seedbed. The eventual development of the rangeland drill made it feasible to seed rough and rocky seedbeds.

CHEATGRASS COMPETITION

The seeding of crested wheatgrass came up against a biological wall on sites infested with the alien annual grass, cheatgrass. In the 1940's it was demonstrated by Robertson and Pearse (1945) that uncontrolled cheatgrass was too competitive to allow the establishment of seedlings of perennial grass seedlings on big sagebrush sites. Detailed studies of the competition between seedlings of cheatgrass and wheatgrass have shown that as few as eight cheatgrass seedlings per 0.1 m^2 would inhibit the establishment of wheatgrass seedlings (Evans 1961). Undisturbed stands of cheatgrass may average 1000 plants per 0.1 m^2.

The principal factor in cheatgrass competition was early season reduction of the limited supplies of available soil water. The nature of competition and the phenology of the weed combined to dictate the possible weed control treatments to reduce competition. If eight cheatgrass seedlings per 0.1 m^2 was sufficient to outcompete wheatgrass seedlings then it was necessary to achieve near-perfect weed control for successful seedings. In arable agriculture, weed control can be achieved by deeply burying ungerminated weed seeds through

mechanical tillage where the surface soil is turned over. This is best, but not completely, accomplished with a moldboard plow. The presence of rocks on many big sagebrush range sites limited the usefulness of moldboard plows. The brushland plow utilizing independently suspended pairs of disk is not efficient at burying the seeds of cheatgrass deep enough to prevent seedling emergence (Young et al. 1969a).

FIRE FOR CHEATGRASS CONTROL

Almost all of the superabundant supply of cheatgrass seeds is located in the litter or on the surface of the seedbed. This would suggest that cheatgrass seeds can be manipulated, but without the option of deep burial by moldboard plowing the alternatives to land managers are limited. Fire is a valid alternative if fuel and fire conditions are correct. There has to be considerable woody fuel present for a fire to burn hot enough to adequately destroy the reserve of cheatgrass seeds (Young and Evans 1978). Even when a dense stand of big sagebrush with a cheatgrass understory burns there will be some viable cheatgrass seeds left on the soil surface in the interspaces between shrubs. The abundance of viable caryopses of cheatgrass after a burn can be judged by examining the ash. If entire caryopses can be identified, even if the lemma and palea are charred, some will be viable and will germinate (Young et al. 1976). Fire is an excellent woody and herbaceous weed control treatment if a hot burn can be obtained safely in a dense stand of big sagebrush with a cheatgrass understory. With a hot fire, the stubs of the big sagebrush plants are consumed to ground level leaving a clean seedbed for drilling. Burning consumes the shrubs and their subcanopy accumulations of litter, but leaves relatively large amounts of nutrients, especially nitrogen, available for use by revegetation species (unpublished research ARS, Reno). The competitive advantage for successful establishment of wheatgrass seedlings is lost if a burned big sagebrush/cheatgrass stand is not seeded the year of the fire. The lack of woody fuel precludes the use of fire as a weed control treatment because the fire from herbaceous fuel is not hot enough to consume cheatgrass seeds.

CHEATGRASS PHENOLOGY

As previously stated, with the exception of fire and mechanical tillage that completely buries seeds on the surface, weed control to reduce competition between cheatgrass and seedlings of perennial grasses is dependent on the germination of the cheatgrass seeds. The seedbank dynamics of cheatgrass must be understood in order to appreciate the nature of the weed control problem. In the late spring when peak plant populations occur there are generally as many viable, but dormant seeds in the litter as there are established plants (Young et al. 1969b). At maturity cheatgrass seeds are generally highly germinable. Seeds that are dispersed in the

seedbed in topoedaphic situations that are not favorable for germination acquire a dormancy over winter. This dormancy breaks down slowly over a 2 to 3 year period (Young and Evans 1975; Evans and Young 1975). The dormant seeds of cheatgrass respond to nitrate and gibberellic enrichment of the seedbed. Because the dormancy gradually breaks down over time, prolonged wet periods with adequate temperatures for germination will result in many more seedlings than when these seeds are exposed to short periods of ideal temperature and moisture conditions.

The germination phenology of cheatgrass seeds varies regionally, sitewise, and annually within sites. In the Pacific Northwest, southern Idaho, and northern California the usual sequence is fall germination with winter top growth confined to a flat rosette of leaves. Root elongation proceeds during the winter, placing the cheatgrass seedlings in an extremely favorable position for competition with seedlings of perennial forage grasses that are planted in the spring (Harris 1967). In the Great Basin on sites where the dominant species of native perennial grass was a _Stipa_ rather than an _Agropyron_, germination of cheatgrass seeds in the fall may occur only once out of every 5 years. Recently we have noted that germination occurs more frequently on sandy situations than on finer textured seedbeds (unpublished research ARS-Reno).

MECHANICAL CONTROL OF CHEATGRASS

The basic mechanical weed control options for cheatgrass becomes tillage in the spring followed by seeding or tillage in the spring with a fallow maintained until the next fall when the site would be seeded. The two treatments have inherent differences that must be understood. The fallow period conserves and stores moisture and allows soil nitrate to accumulate (Eckert et al. 1970).

Moisture and nitrate availability both interactively influence the establishment of perennial grass seedlings. Too much nitrate will produce more harm than good in dry years and when cheatgrass control is not complete enough to prevent preemption of the available water and nitrate by the weed (Kay and Evans 1965). Moisture and nitrate accumulations on fallows influence the germination characteristics of the viable, but dormant seeds of cheatgrass in the seedbank and foster the germination of alternative floras from lower successional levels that have been previously suppressed by the growth of cheatgrass.

Spring tillage followed directly by seeding has little influence on the dormant seedbank of cheatgrass other than by physically modifying the surface of the seedbed. Generally, the implement most adapted to spring tillage is a light disk harrow with minimum draft requirements. Complete turnover of the seedbed would give maximum establishmnt of perennial grass stands. This is not practical on most rangeland sites and may not

be economically feasible because of the draft requirement of a moldboard plow even on sites where it is physically possible.

Tillage for weed control on rangelands seldom involves secondary tillage to enhance seedbed quality. The bulk density and aggregate particle size and consistency of seedbeds may be highly variable among soils and are greatly affected by soil moisture conditions within soils. Unless such differences can be compensated for in the drilling process, stand establishment of the seeded perennial grasses will suffer, even to the point of being greatly reduced. A small amount of time spent in additional seedbed preparation may mean the difference between seedling stand success or failure.

The problem with mechanically maintained fallows centers on the occurrence of alternate floras that are conditioned by summer moisture events. Russian thistle (Salsola australis = S. iberica = S. kali, etc.) is a major problem on fallows. If the summer stays dry, no follow-up mechanical weed control will be necessary. If repeated summer rains occur, subsequent weed control will be necessary.

HERBICIDAL CONTROL OF CHEATGRASS

Range managers barely had started to approach the mechanical control of cheatgrass when herbicides were introduced into American agriculture. There was considerable research effort on western rangelands to find a herbicide for the selective control of halogeton. It did not take long for this technology to be tested for control of cheatgrass. The constraints of the environment and the weed species channeled herbicidal treatments into two categories: (1) fallows created with soil-active herbicides, and (2) control by contact herbicides directly followed by seeding. A physiologically selective herbicide for pre- or post-emergence weed control of cheatgrass in seedling stands of wheatgrass was never developed.

Herbicidal fallows require that the spectrum of weed control activity of the herbicide be balanced with its residual half life (Evans et al. 1969). Cheatgrass usually dominates the seral continuum of annuals in big sagebrush plant communities, but there are often a few plants of tumble mustard (Sisymbrium altissimum L.) tansy mustard [Descurainia pinnata (Walt.) Britton] and the ever present Russian thistle to contend with and to control during the summer.

Atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] proved to be the best adapted herbicide for weed control and soil persistence for cheatgrass control on big sagebrush sites (Evans et al. 1969). The treatment sequence consists of applying the atrazine in the fall, resulting in complete vegetation control during the next growing season, and then seeding the following fall (Eckert and Evans 1967). Weed control generally was good with the atrazine fallow treatment. Residues of atrazine were troublesome at times in reducing seedling stands of perennial grasses, depending on herbicide application rate, the amount of moisture received, and soil type (Eckert et al. 1972). Seeding with a deep furrow drill to move surface herbicide residues between rows was effective in reducing damage to grass seedlings (Eckert 1974, Asher and Eckert 1973). The atrazine application did not control established perennial grasses so the method naturally led to a procedure for enhancing thin or suppressed stands of wheatgrass by reseeding sites after weed control (Eckert 1979).

During the seedling year for the wheatgrass seedlings, a flora of broadleaf weeds often occurred on the seedbeds. These species could be selectively controlled with an application of 2,4-D [(2,4-dichlorophenoxy)acetic acid]. The removal of a broadleaf seedling from a seedling stand of wheatgrass was simple compared to the attempted selective removal of cheatgrass from wheatgrass seedling stands.

The one-year fallow treatment was not sufficient to completely deplete the seedbank of cheatgrass. The fallow period did result in the complete decay of litter on the surface of the seedbed. This left the cheatgrass caryopses exposed on the surface of the seedbed in a microenvironment capable of supporting only limited germination (see Evans and Young and Young et al. this volume). Essentially, weed control was accomplished by modifying the capacity of the seedbed to support cheatgrass germination. During springs with prolonged periods of moisture the microenvironment of the seedbed is brought within the potential of cheatgrass to germinate plus the prolonged germination period allows time for more cheatgrass seeds to break dormancy.

The atrazine fallow system is highly adapted to sites of lower potential. The moisture and nitrate accumulations on those poor sites during the fallow year can contribute to exceptional results. Through this weed control and revegetation system it is possible to establish wheatgrass plants on sites with too little environmental potential for them to persist. This is despite the general ecological principle that seed germination and seedling establishment are the weakest links in plant dominance of sites.

The herbicidal alternative to spring tillage and seeding involved application of the herbicide, paraquat (1,1'-dimethyl-4,4'-bipyridinium ion) (Evans et al. 1967). Paraquat has the unique characteristic of being tied up on soil particles as soon as it touches the mineral soil. This permits near simultaneous herbicide application and seeding. Paraquat was not effective on seedlings of tansy mustard hence the inclusion of small amounts of 2,4-D is necessary in the herbicide application for control of this species.

Weed control systems have been developed in which herbicidal control of herbaceous weeds and big sagebrush are combined with seeding of perennial

grasses and other forage species (Evans and Young 1977). All of these mechanical or herbicidal weed control systems involved exclusion of grazing through the seedling year for the perennial grass and usually past seedripe for the two year old seedlings. Grazing management, as a weed control method, has not been found successful for cheatgrass control in the sagebrush environment because of the nature of competition. In other annual grass dominated communities where light is a dominant factor in competition, grazing may be helpful for establishment of seedlings of forage species even after initial herbicidal weed control (Evans et al. 1975).

SYNTHESIS

A common thread ties together all of the successful weed control-seeding methods that we have discussed - it is that the basis for their success lies in the alteration of the seedbed microenvironment to discourage weeds and promote the establishment and growth of forage species. Brush and weed control are necessary and integral parts of forage establishment, and like seeding and seedbed preparation, can be considered important factors altering seed and seedbed dynamics on rangelands.

LITERATURE CITED

Asher, J.E. and R.E. Eckert, Jr. 1973. Development, testing, and evaluation of the deep furrow drill arm assembly for the rangeland drill. J. Range Manage. 26:377-379.

Eckert, R.E., Jr. 1974. Atrazine residue and seedling establishment in furrows. J. Range Manage. 27:55-56.

Eckert, R.E., Jr. 1979. Renovation of sparse stands of crested wheatgrass. J. Range Manage. 20:35-41.

Eckert, R.E., Jr. and R.A. Evans. 1967. A chemical fallow technique for control of downy brome and establishment of perennial grasses on rangeland. J. Range Manage. 20:35-41.

Eckert, R.E., Jr., G.J. Klomp, J.A. Young, and R.A. Evans. 1970. Nitrate-nitrogen status of fallowed rangeland soils. J. Range Manage. 23:445-447.

Eckert, R.E., Jr., G.J. Klomp, R.A. Evans, and J.A. Young. 1972. Establishment of perennial wheatgrasses in relation to atrazine residue in the seedbed. J. Range Manage. 25:219-224.

Evans, R.A. 1961. Effects of different densities of downy brome (Bromus tectorum L.) on growth and survival of crested wheatgrass (Agropyron desertorum) in the greenhouse. Weeds 9:216-223.

Evans, R.A., R.E. Eckert, Jr., B.L. Kay, and J.A. Young. 1969. Downy brome control by soil active herbicides for revegetation of rangelands. Weed Sci. 17:166-169.

Evans, R.A., B.L. Kay, and J.A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. Hilgardia 43:79-102.

Evans, R.A. and J.A. Young. 1975. Enhancing germination of dormant seeds of downy brome. Weed Science 23:354-357.

Evans, R.A. and J.A. Young. 1977. Weed control-revegetation systems for big sagebrush-downy brome rangelands. J. Range Manage. 30:331-336.

Evans, R.A., R.E. Eckert, Jr., and B.L. Kay. 1967. Wheatgrass establishment with paraquat and tillage on downy brome ranges. Weeds 15:50-55.

Harris, G.A. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. E. Col. Mono.: 89-111.

Heady, H.F. and J. Bartolome. 1977. The Vale rangeland rehabilitation program: The desert repaired in southeastern Oregon. U.S. Forest Service Res. Bull. PNW 70. Pacific Northwest Forest and Range Exp. Sta., Portland, OR.

Kay, B.L. and R.A. Evans. 1965. Effects of fertilization on a mixed sand of cheatgrass and intermediate wheatgrass. J. Range Manage. 18:7-11.

Robertson, J.H. and C.K. Pearse. 1945. Artificial reseeding and the closed community. Northwest Sci. 19:58-66.

Young, J.A. and R.A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. Weed Sci. 23:358-364.

Young, J.A. and R.A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. J. Range Manage. 31:283-289.

Young, J.A. and R.A. Evans. 1986. History of crested wheatgrass. pp. 21-22. Proc. Crested Wheatgrass - Its Values, Problems, and Myths. Symposium Proceedings. Utah State University, Logan, UT.

Young, J.A., R.A. Evans, and R.E. Eckert, Jr. 1969a. Emergence of medusahead and other grasses from four seeding depth. Weed Sci. 17:376-379.

Young, J.A., R.A. Evans, and R.E. Eckert, Jr. 1969b. Population dynamics of downy brome. Weed Sci. 17:20-26.

Young, J.A. and D. McKenzie. 1982. Rangeland
    drill. Rangelands 4:108-113.

Young, J.A., R.A. Evans, and R.A. Weaver. 1976.
    Estimating potential downy brome competition
    after wildfires. J. Range Manage. 29:333-
    337.

SEEDING ON OR NEAR THE SURFACE OF SEEDBEDS
IN SEMIARID ENVIRONMENTS

James A. Young[1], Raymond A. Evans[2],
and Greg J. Cluff[3]

ABSTRACT

Moisture and temperature relations interact to
make it difficult for seeds to germinate on the
surface of seedbeds. The exposed portion of the
seed loses moisture if there is a negative
gradient to the atmosphere. At the same time,
moisture uptake from the substrate is limited by
the points of contact with the seed coat.

INTRODUCTION

The surface of seedbeds presents a paradox for
seeds and for planters of seeds. The closer a
germinating seed is located to the surface of a
seedbed, the less energy must be expended for
emergence and the subsequent initiation of
photosynthesis that leads to seedling
establishment. The closer a seed is located to
the surface of a seedbed, the greater the
potential for diurnal fluctuations of the physical
environmental parameters. The particles of soil
and the interspacial soil solutions and/or soil
atmosphere act as an insulating barrier that
dampens extremes in soil temperature and
therefore, the liquid and atmospheric water
relations in the surface soil (Chippindale 1949).

Generally, the ideal seedbed is one where the seed
is covered with soil particles and the particles
are firmly packed around the seed to ensure
hydraulic conductivity of moisture from the soil
matrix to the seed (Collis-George and Sands
1959). A seed exposed on the surface of a seedbed
obviously has reduced area of contact between the
particles of the germination substrate and in
addition, the exposed portion of the seedcoat is
open to moisture loss to the atmosphere if a
negative gradient exists from the moisture
equilibrium of the hydrating seed to the
atmosphere (Harper et al. 1965). Obviously, it
would seem advantageous for seeds to strike a
balance between burial and energy requirements for
emergence. The ideal depth is proportionately
related to the energy reserves of the seed which
is roughly indicated by seed size. In range
revegetation activities, these relations are often
expressed by the observation that small seeded
species are difficult to establish by direct
seeding because they must be seeded at a shallow
depth.

[1]Range Scientist, Agricultural Research Service,
U.S. Dept. Agric., 920 Valley Road, Reno, NV.
[2]Range Scientist, retired, 1560 California,
Reno, NV.
[3]Plant Breeder, 601 Oswell St., Bakersfield, CA.

However, many rangelands are not tillable and
chances for seedbed preparation are minimal.
Therefore, range managers are often interested in
broadcasting without physically covering the
seeds.

Besides the necessity of broadcasting seeds where
seedbeds can not be prepared, there are certain
types of seeds that must be seeded on the surface
of seedbeds because of physiological restrictions
in the inherent biological systems of the seeds
themselves. These physiological systems include
1) germination requirements for light and/or
specific light quality, 2) requirements of
fluctuating temperatures for germination, 3) near
complete lack of seed reserves which makes near
instant establishment necessary, and 4) other
undefined physiological requirements that
precondition germination to the surface of
seedbeds. Essentially, the paradox of seeding on
the surface of seedbeds resolves itself into a
triangle, the points of which are 1) most seeds
germinate and establish best when buried at a
proper depth in a firm seedbed; 2) range managers
are often forced to try to seed on the surface of
seedbeds because of the inability to prepare
seedbeds; and 3) some seeds, for different
physiological reasons, must be seeded on the
surface of seedbeds.

Nature of the Surface of the Seedbed

The thinnest possible seed coverage with soil
particles greatly enhances the germination of many
seeds. If the osmotic potential of the soil
solution is not reduced by soluble salts, moisture
potential during the germination process for the
buried seeds are governed by matric potential or
how strongly the film of soil moisture is held to
the soil particles and hydraulic conductivity from
the soil particles to the seedcoat (Collis-George
and Hector 1966). Hydraulic conductivity is
governed by the size of the soil particles in the
germination substrate, the bulk density of the
seedbed, and the soil water content. Several
other papers in this symposium address this
substrate-seed moisture relationship (Evans and
Young 1987a, 1987b; Frasier 1987).

The moisture relations of a seed lying on the
surface of a flat seedbed are dramatically altered
by soils of different textures. On a coarse sand,
there are relatively few points of contact
between the seedcoat and the sand particles. On a
fine textured clay soil, the seed has many more
points of contact with the soil substrate. The
soil moisture is held tightly to the clay
particles, but the soil capillaries are much
finer. However, clays that expand and contract in
the course of wetting and drying may leave seeds
in a pedestalled situation that is more harsh than
the coarse sand seedbed (Koller and Hadas 1982).

Obviously, most seedbeds are not perfectly flat,
but consist of various levels and types of surface
microtopography with the potential for various
levels of litter accumulation. The moderating
influence of litter and microtopography on the

potential of the surface of seedbeds is covered in this symposium (Evans and Young 1987a).

The atmospheric portion of the moisture relations of the surface of seedbeds is the least understood and apparently an important part of the equations governing germination in this environmental situation. If the atmosphere around the seed is at or very near saturation, the seed will apparently not suffer undue moisture stress. Care should be taken in interpreting this phenomena, because the energy requirements in overcoming moisture deficits, even close to saturation, may be significant (e.g. see Young et al 1983). Many of our western range areas have relative humidities that are far below saturation, even under most favorable conditions. As rangeland environmental conditions become increasingly arid, seeds on the soil surface are exposed to prolonged periods of desiccation and shorter periods of atmospheric saturation. In temperate deserts, seeds on the surface of seedbeds are exposed to prolonged periods of frost and desiccation in a form of freeze drying. This may result in biophysical changes in inherent potential of seeds to germinate (Young et al 1969).

The general rule-of-thumb for seeding depth for seeds is two and one half times their diameter. In the case of grass caryopses, this would be more applicable to length than diameter. A grass caryopse 1 cm in length would be planted $2\frac{1}{2}$ cm deep in the seedbed. There are many exceptions to this rule. Seeds of Indian ricegrass [Oryzopsis hymenoides (R.& S.) Ricker] have highest establishment when planted 15 cm deep in nearly pure sand seedbeds in the desert (unpublished research, ARS-Reno). The seeds of Indian ricegrass are only 3 mm long.

Escape from the Surface of Seedbeds

In rangeland situations, there are a number of plant species that have evolved mechanisms for seed burial. The geranium family is especially noted for species with seeds adapted for self burial. Erodium botrys (Cov.) Bertol provides a good example for the family (Young et al. 1975). Long styles persist and remain attached to the fruit coat. At maturity, the styles become tightly coiled. When the fruits disperse from the plant to the seedbed, the styles coil and uncoil in response to changing relative humidity and temperature. This coiling action drives the sharpened calus end of the fruit into the surface soil. The fruit is driven to the length of the partially coiled style, which is apparently the optimum depth for burial, at which point the style snaps off the fruit. The self-burial action also ruptures the seedcoat within the fruit, which permits germination of the otherwise hardseeded, dormant seeds. The self-burial mechanism for Erodium seeds is so effective in placing the seeds in desirable positions for germination that plants of these species are among the first to emerge and become established on the annual-dominated ranges of California west of the Sierra Nevada (Young et al. 1981).

Caryopses with twisted geniculate awns occur with numerous species of grasses. This characteristic is particularly well-developed among species of Stipa. Awns for self-burial of grass caryopses do not have to have conspicuous appendages. In the case of Aira caryophyllea L., the awn is only 4 to 6 mm long, but it drives the calus end of the caryopses into the surface soil (Evans et al. 1976). A characteristic of Aira caryopses and many other seeds of fruits that have self-burial mechanisms is the presence of a hard, sharp calus surrounded with rings of stiff, backward pointing hairs that prevent the seed from being pulled out of the soil by a drying, twisting awn. The harsh, surface environment of seedbeds is modified by large numbers of species in diverse families through the mechanism of seed mucilage (Young and Evans 1973). Apparently, seed mucilage can serve the dual function of increasing hydraulic conductivity from the germination substrate while reducing moisture loss to the atmosphere (Harper and Benton 1966). There are so many different types of mucilaginous seeds that it is highly probable that the mechanism has functioned as a selective advantage in many different forms.

The problem of self-burial to avoid the surface of seedbeds is circumvented by species which produce subterraneum fruit, as in the case of Trifolium subterraneum L. Such mechanisms apparently limit seed dispersal to enhance the chances of a desirable germination habitat.

The caching activities of birds and small mammals often ensure that the seeds of many different species are buried in environments that have desirable conditions for germination (e.g. McAdoo et al. 1983). The efficiency of such co-evolved systems depends on seed consumption losses and on how desirable the cache environment is for seeding establishment.

Seeds with Light Requirements

The seeds of many species require light for germination (Anon. 1981). The level of the germination response to light varies greatly among species. Light may be an absolute requirement for germination, or it may enhance the rate or total amount of germination. Often seeds are sensitive to the quality of light with near red light enhancing and far red light prohibiting germination (Toole et al. 1956). Seeds may also be sensitive to photoperiod.

If seeds are entirely buried in the soil, they receive very little light of sufficient quality to trigger phytochrome reactions in seeds. This means that seeds that require light for germination are largely restricted to germination on the surface of seedbeds. The seedbed does not have to be bare, nor does it have to be smooth. Litter and microtopography are probably essential in semiarid to arid environments for seeds of light-sensitive species to germinate. It is possible for seeds to germinate in litter without being in contact with mineral soil (Young et al.

1971). Light-requiring seeds can have copious amounts of seed mucilage and be able to germinate on the surface of seedbeds as is the case for seeds of Salvia aethiopis (unpublished research, ARS-Reno).

Seeds that Require Fluctuating Temperatures to Germinate

Seeds of Distichlis spicata Torr. do not require light for germination, but they are highly dormant unless exposed to widely fluctuating temperatures. Most collections of this species were determined to germinate best at 15/40 C (15 C for 16 hr and 40 C for 8 hr in each 24 hr period) temperature regimes (Cluff et al. 1983). Maximum germination was obtained with one source of seed at a 10/50 C regime. A diurnal temperature fluctuation of at least 20 C was required to obtain more than 10 percent germination with Distichlis spicata seeds.

Frequently, there is an interaction between the light quality requirements of seeds for germination and widely fluctuating temperatures (Toole et al. 1955). In the case of seeds of Verbascum thapsus L., germination is restricted to the dark and to very high temperatures (Semenza et al. 1978). With the addition of filtered near red light, germination will also occur with widely fluctuating temperatures. Even such extremes in diurnal fluctions as 0 C night and 40 C day temperatures produce germination in the presence of filtered near-red light.

There are many studies which show the close interaction between sensitivity to light quality and fluctuating temperatures to enhance germination. In some cases a nitrate ion source, such as potassium nitrate (KNO_3), further enhances germination (Taylorson 1969). In other cases, gibberellin plus KNO_3 enrichment of the germination substrate can be substituted for light requirements for germination (Young and Evans 1969).

Seeds with Minimum Stored Reserves

Seeds of Salsola australis R. Br. (equals S. iberica) provide a classic example of high risk reproductive strategy. The seeds of S. australis consist of a tightly coiled embryonic plant with virtually no stored reserves of energy to support the seedling until it becomes established.

Seeds of S. australis can initiate germination and become established during the course of a rainstorm if temperature conditions and the internal time clocks of the physiological systems of the seeds are in synchronization (Wallace et al. 1968). At maturity, seeds of S. australis will only germinate at a narrow range of very specific temperatures (Young and Evans 1972). Gradually over winter, the temperature restrictions for germination disappear and after the danger of frost in the spring, seeds of S. australis will germinate at virtually any

conceivable seedbed temperature, including -2 C alternating with 50 C. In order for this type of germination strategy to have any chance of success, each plant must produce huge numbers of seeds and the species must have a highly efficient seed dispersal system. Germination at the surface of a seedbed seems to be a facultative requirement for seeds of other chenopods, such as Kochia prostrata L. or Ceratoides lanata (Pursh) Howell (Dettori et al. 1984 and Young et al. 1981).

Nature of Fluctuating Seedbed Temperatures

In a temperate desert situation with late fall or early spring germination, the key temperatures for surface germination are -2 to 2 C at night alternating with at least 20 C during the day (Evans et al. 1970). As the daytime temperature increases to the 30 or 40 C range, the environment of the surface of seedbeds becomes more severe. Essentially, the extremely fluctuating temperature category for this environment is 0/20 or 2/20 C through 0/40 and 2/40 C (Young and Evans 1982). For nighttime temperatures to drop markedly lower than the 0 C for prolonged periods, ice crystals would form from the soil moisture. This requires a prolonged period of air temperatures well below 0 C.

When you compare the germination profiles of seeds of selected perennial grasses that are seeded on temperate desert rangelands, some interesting trends become apparent (Table 1). The cultivars of crested wheatgrass Fairway [Agropyron cristatum (L.) Gaertn.] and Nordan (A. desertorum Fisch. ex Schult) illustrate the basic cool-season perennial grass germination responses. At the core regimes of the profile, which are known as the moderate seedbed temperatures, average germination jumps to about 70 percent. At widely fluctuating seedbed temperatures, those that characterize the surface of seedbeds, there is a disparity between the two cultivars in that the smaller sized caryopses of Fairway' average over 70 percent germination, while 'Nordan', which was selected for larger sized caryopses, averages only slightly over 50 percent.

The widely fluctuating temperature regimes are actually composed of roughly one third warmer and two thirds colder than moderate incubation temperatures, depressing the germination of seeds of 'Fairway' and 'Nordan' to an average of 77 and 53 percent of that observed at moderate temperatures, respectively. Warmer incubation temperatures depress average germination to roughly 60 percent and colder temperatures to 50 percent of that observed at moderate temperature. For seeds of 'Nordan' crested wheatgrass, the observed mean germination for the widely fluctuating temperature regimes is roughly the weighted average of germination in the colder and warmer incubation categories. However, for seeds of 'Fairway' crested wheatgrass, the reduction in germination at fluctuating temperatures as compared to moderate temperatures is roughly 10 percent less than the weighted averages of cooler and warmer regimes.

Table 1. Comparison of mean germination at standard 55 temperature profile, germination at colder, widely fluctuating, and warmer temperatures for a range of cool-season perennial grasses commonly seeded on temperate desert rangelands and for Bromus tectorum (Young and Evans 1982)[1]

Scientific name[2]	Cultivar	Mean	Moderate	Colder	Widely Fluctuating	Warmer
					Percent of moderate temperature germination	
			%			
Agropyron cristatum	Fairway	56 c	70 c	57	77	66
Agropyron desertorum	Nordan	49 c	73 bc	37	53	60
Elytrigia pontica	Jose	64 b	88 ab	38	73	61
Festuca ovina	Covar	49 c	78 bc	59	51	23
Poa Canbyi	Canbar	34 d	52 d	67	48	19
Psathyrostachys juncea	Vinall	60 bc	82 bc	34	64	70
Bromus tectorum		82 a	93 a	73	90	75

[1] Means within columns followed by the same letter are not significantly different at the 0.01 level of probability

[2] Nomenclature follows that of Dewey (1983)

Better germination at widely fluctuating temperatures than would be indicated by colder and warmer mean germination is also apparent for the large seeds of 'Jose' tall wheatgrass [Elytrigia pontica (Podp) Holub] (Table 1). The diurnal fluctuations of a 16 hr cold and 8 hr warm period are apparently beneficial to some part of the biochemical processes that we know in total as seed germination.

The caryopses of 'Covar' sheep fescue (Festuca ovina L.) and 'Canbar' canby bluegrass [Poa canbyi (Scribn.) Piper] are both quite small and therefore, must be seeded at shallow depths. The caryopses of both of these species have substantial germination at colder than moderate incubation temperatures, but have very low germination at warmer than moderate incubation temperatures. Seeds of these two species should be seeded early in the spring to avoid the germination repression of the warmer portion of the fluctuating temperature regimes.

Russian wildrye (referred to by Asay as Psathyrostachys juncea Nevski) is another perennial grass with relatively small caryopses that must be planted at shallow depths and has the reputation of being difficult to establish on temperate desert rangelands. In contrast to 'Covar' sheep fescue and 'Canbar' canby bluegrass, the seeds of 'Vinall' Russian wildrye have germination greatly reduced by colder than moderate incubation temperatures, with warmer than moderate temperature regimes producing 70 percent of the germination observed at moderate regimes.

Bromus tectorum L. provides a bottom line for any attempts to revegetate in temperate desert plant communities. The seeds of this weed are highly viable and adverse incubations, including widely fluctuating temperatures, are not that detrimental to its germination.

Temperatures are only a portion of the environments of the surfaces of seedbeds. Interpretation of the results of temperature germination profiles must always be made with the interacting influence of moisture availability in mind.

LITERATURE CITED

Anon. 1981. Rules for testing seeds. Proceedings of the Association of Official Seed Analysts. 20(2)1-125.

Chippindale, H.G. 1949. Environment and germination in grass seeds. J. British Grassland Soc. 4:57-61.

Cluff, G.J., R.A. Evans, and J.A. Young. 1983. Desert saltgrass seed germination and seedbed ecology. J. Range Manage 36:419-422.

Collis-George, N. and J.B. Hector. 1966. Germination of seeds as influenced by matric potential and by area of contact between the seed and soil water. Austral. J. Soil Res. 4:145-165.

Collis-George, N. and J.E. Sands. 1959. The control of seed germination by moisture as a soil physical property. Aust. J. Agric. Res. 10:628-636.

Dettori, M.L., J.F. Balliette, J.A. Young, and R.A. Evans. 1984. Temperature profiles for germination of two species of winterfat. J. Range Manage. 37:218-222.

Dewey, D.R. 1983. Historical and current taxonomic perspectives of Agropyron, Elymus, and related genera. Crop Science 23:637-642.

Evans, R.A., H.R. Holbo, R.E. Eckert, Jr. and J.A. Young. 1970. Functional environment of downy brome communities in relation to weed control and revegetation. Weed Science 18:154-162.

Evans, R.A. and J.A. Young. 1987a. Seed germination and seedling emergence of rangeland plants in relation to seedbed temperature and available water. pp. __. In G.W. Frasier and R.A. Evans (ed) Seed and Seedbed Ecology of Rangeland Plants, Agric. Res. Serv., U.S. Dept. of Agric. Washington, D.C.

Evans, R.A. and J.A. Young. 1987b. Seedbed modification with weed control and seeding. pp. __ In G.W. Frasier and R.A. Evans (ed) Seedbed Ecology of Rangeland Plants. Agric. Res. Serv., U.S. Dept. of Agric. Washington, D.C.

Evans, R.A., J.A. Young, and B.L. Kay. 1976. Germination of winter annual species from a rangeland community treated with paraquat. Weed Science 22:185-187.

Frasier, G.W. 1987. Soil moisture and wet-dry cycle effects on seed germination and seedling establishment. pp. __. In G.W. Frasier and R.A. Evans (ed) Soil Moisture Availability Effects on Seed Germination and Germinated Seed Survival of Warm Season Grasses. Agric. Res. Ser., U.S. Dept. Agric. Washington, D.C.

Harper, J.L., J.T. Williams, and G.R. Sagar. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants. J. Ecol. 53:273-286.

Harper, J.L. and R.A. Benton. 1966. The behavior of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. J. Ecol. 54:151-166.

Koller, D. and A. Hadas. 1982. Water relations in germination of seeds. pp. 401-431. In: O.L. Lange et al. Physiological plant ecology II. Water relations and carbon assimilation. Encyclopedia of plant physiology. New Series. volume 12 B. Springer-Verlag, New York.

McAdoo, J.K., C.C. Evans, B.A. Roundy, J.A. Young, and R.A. Evans. 1983. Influence of heteromyid rodents on Oryzopsis hymenoides germination. J. Range Manage. 36:61-64.

Semenza, R.J., J.A. Young. and R.A. Evans. 1978. Influence of light temperature on the germination and seedbed ecology of common mullein. Weed Sci. 26:577-581.

Taylorson, R.B. 1969. Photo control of rough cinquefoil seed germination and its enhancement by temperature manipulation and KNO_3. Weed Sci. 17:144-148.

Toole, E.H., S.B. Hendricks, H.A. Borthwick, and V.K. Toole. 1956. Physiology of seed germination. Annual Review Plant Physiology 7:299-324.

Toole, E.H., V.K. Toole, H.A. Borthwick, and S.B. Hendricks. 1955. Interaction of temperature and light in germination of seeds. Physiol. 30:473-478.

Wallace, A., W.A. Rodes, and E.F. Frolich. 1968. Germination behavior of Salsola as influenced by temperature, moisture, depth of planting, and gamma radiation. Agron. J. 60:267-268.

Young, J.A. and R.A. Evans. 1969. Control and ecological studies of scotch thistle. Weed Sci. 17:60-63.

Young, J.A. and R.A. Evans. 1972. Germination and establishment of Salsola in relation to seedbed environment. Part II. Seed distribution, germination, and seedling growth of Salsola and microenvironmental monitoring of the seedbed. Agron. J. 64:219-222.

Young, J.A. and R.A. Evans. 1973. Mucilaginous seedcoats. Weed Sci. 21:52-54.

Young, J.A. and R.A. Evans. 1982. Temperature profiles for germination of cool season range grasses. ARR-W-27. Agr. Res. Ser., U.S. Dept. Agric., Oakland, CA. 98 p.

Young, J.A., R.A. Evans, and R.E. Eckert, Jr. 1969. Population dynamics of downy brome. Weed Sci. 17:26-26.

Young, J.A., R.A. Evans, and B.L. Kay. 1971. Germination of caryopses of annual grasses in simulated litter. Agronomy J. 63:551-555.

Young, J.A., R.A. Evans, and B.L. Kay. 1975. Dispersal and germination dynamics of broadleaf filaree (Erodium botrys (Cav.) Bertol). Agron. J. 67:54-57.

Young, J.A., R.A. Evans, C.A. Raguse, and J.R. Larson. 1981. Germinable seeds and periodicity of germination in annual grasslands. Hilgardia 49:1-37.

Young, J.A., R.A. Evans, B.A. Roundy, and C.J. Cluff. 1983. Moisture stress and seed germination. ARM-W-36. Agric. Res. Serv., U.S. Dept. Agric., Berkeley, CA.

Young, J.A., R.A. Evans, R. Stevens, and R.L. Everett. 1981. Germination of Kochia prostrata seeds. Agron. J. 73:957-961.

ALLELOPATHIC EFFECTS OF PINYON AND JUNIPER LITTER ON EMERGENCE AND GROWTH OF HERBACEOUS SPECIES

Richard L. Everett[1]

ABSTRACT

Singleleaf pinyon (Pinus monophylla) and Utah juniper (Juniperus osteosperma) litter reduced seedling emergence from buried seed. Activity of allelopathic chemicals was restricted to the needle litter layer. Seed desiccation was probably more critical to seedling emergence than allelopathic effects. Inhibition of commonly seeded species by tree litter should be considered in seedings.

INTRODUCTION

The most critical stage in the life cycle of a plant is initial plant establishment (Harper 1977). The ability to inhibit establishment of competing plants would be advantageous to woodland species where water resources are limited. Allelopathy, the chemical inhibition of one plant by another, is one means of restricting establishment of potential competitors. Indigenous understory species are excluded from canopy litter zones of singleleaf pinyon (Pinus monophylla Torr. and Frem.) and Utah juniper (Juniperus osteosperma Torr.) before and after tree harvest. Species seeded into tree harvested sites showed variable emergence and growth response in tree litter zones (Everett 1979). Natural response and seeding studies suggests allelopathic mechanisms may be at work in Great Basin woodlands (Everett et al. 1984, Everett and Sharrow 1984).

This paper reports results of greenhouse studies that tested these hypotheses: (1) pinyon litter chemically or physically inhibits emergence and growth of indigenous grass species, and (2) emergence of broadcast and buried seed of commonly seeded grasses and forbs is inhibited by Utah juniper and singleleaf pinyon litter. Results of this study help explain observed understory patterns and provide information on appropriate species for seeding cut-over woodlands.

BACKGROUND

In pinyon and juniper woodland succession most species are present on sites immediately after disturbance and succession is more a series of pattern changes than changes in species (Everett and Ward 1984). Understory species form distinct zones around trees and these zones expand with tree growth (Arnold 1964, Johnsen 1962)

Understory is often excluded or significantly reduced in litter zones under tree crowns in the Great Basin (Everett et al. 1984). These litter zones are composed of a surface layer of loose, freshly fallen litter and a lower amorphous fermentation layer of decomposing needles (Wright 1973)[2]. Because litter zones can occupy more than 50 percent of the soil surface in closed stands (Everett and Koniak 1981), the exclusion of understory has both ecological and range management consequences.

In closed stands, few understory seeds (0.4 seeds/dm^2) fall in the litter zone under trees and establishment of new perennial plants is rare (Everett and Sharrow 1983). When trees are removed, seed rain to the litter increases by an order of magnitude (37 seeds/dm^2), but seedling establishment of most understory species still does not occur (Everett and Sharrow 1984). Bottlebrush squirreltail (Sitanion hystrix Nutt.) and cheatgrass (Bromus tectorum L.) are exceptions; they readily establish in tree litter following tree removal.

Lack of understory in the litter layer could be the result of tree-understory competition, the physical and chemical inhibition of seedling establishment by needle litter, or both (Anderson et al. 1969). Because herbaceous species do not readily establish in needle litter following tree removal we can discount competition for light, nutrients, and soil water as factors initially controlling understory establishment. Soil moisture and nutrients are greater under the litter layer than in the interspaces between cut stumps (Everett and Sharrow 1985, Everett et al. 1986). Allelopathy, physical impedance, or some other unidentified cause appear to be restricting understory establishment.

Jameson (1961, 1966) and Lavin et al. (1968) demonstrated leachates of Utah juniper and pinyon (Pinus edulis Engelm.) foliage inhibited germination of associated understory species in laboratory tests. Essential oils, a-pinene, b-pinene, and limonene, found in foliage of singleleaf pinyon (Scholl and Shafizadeh 1977)[3] have allelopathic properties (Rice 1974). Whether these allelopathic chemicals affect understory establishment in litter or soil seed beds is unknown.

---

[2]Wright, D. A. 1973. Decomposition of Pinus monophylla Torr. and Frem. needle litter and associated fungi in a pinyon-juniper community in western Nevada. Univ. of Nev./Reno. M. S. thesis. 94 p.

[3]Scholl, J. P. and F. Shafizadeh. 1977. Extractive content of Pinus monophylla from Nevada. Final Report, Nevada Division of Forestry. Coop. Agree. 12-11-204-1. Mimeo. 8 p.

MATERIALS AND METHODS

Indigenous Grass Species Trials

A pot study testing emergence and growth of four grass species in three seed beds was established under greenhouse conditions using a completely randomized design. There were four replicates of the experimental unit, a planting pot (10 x 10 x 5 cm) containing 50 seeds of a single species in a uniform seedbed.

Seeds bottlebrush squirreltail (SIHY), Idaho fescue (Festuca idahoensis Elmer) (FEID), Sandbergs bluegrass (Poa sandbergii Vasey) (POSA), and cheatgrass (BRTE) were collected from woodland sites in central Nevada. Seeds were cleaned and high-graded to select the heaviest filled seed for seeding trials.

Pinyon litter from the fermentation layer, mineral soil from under litter (0- to 5- cm depth), and mineral soil from interspace soils (0- to 5- cm depth) between trees were used as seedbeds for each species. The amorphous needle mass was broken up into friable components and both litter and mineral soils sifted to pass through a 2-mm mesh screen. Approximately 500 cm³ of seedbed material was placed in each pot.

Filled pots were watered for one week to germinate soil seed reserves and emerging plants were removed. Pots were then seeded with one of the four indigenous grass species. Seeds were buried 0.5 cm below the soil or litter surface. Seedling emergence at greenhouse air temperatures of 10 to 20 °C was recorded weekly for six weeks. Seedlings were considered to have emerged when leaves were at least two cm tall. Emerging seedlings were transferred into a duplicate set of pots until each pot contained 10 seedlings. Seedlings were thinned to four plants per pot after six weeks, harvested four months after planting. Soil was washed from the roots, and roots and shoots were oven dried at 47°C before weighing.

Seedling emergence and shoot-root weights from litter and mineral soil seedbeds were compared in analysis of variance tests. Hartley's sequential method of testing was used to separate means at the p=0.05 level (Snedecor and Cochran 1978).

The seedling emergence component of the study was repeated using the same understory species, but loose needle litter was substituted for amorphous litter from the fermentation layer. Emergence of seeded species was observed for nine weeks and results analyzed as previously described.

Commonly Seeded Species Trials

This greenhouse pot experiment tested emergence of five commonly seeded species in three seed beds: (1) pinyon litter over mineral soil, (2) juniper litter over mineral soil, and (3) mineral soil. Seeds were buried or broadcast on the soil surfaces.

A completely randomized design was used with four replicates of the experimental unit. The experimental unit was a planting pot containing 50 seeds of a single species broadcast or buried in a uniform seed bed.

Commercial seeds of smooth brome (Bromus inermis Leyss.)(BRIN), Fairway crested wheatgrass (Agropyron cristatum L. Gaertn.) (AGCR), alfalfa (Medicago sativa L.'Ladak') (MESA), blue flax (Linum lewisii Pursh) (LILE), and small burnet (Sanquisorba minor Scop.) (SAMI) were high-graded to select the heaviest filled seed for seeding trials. Planting pots (10x10x5 cm) were filled with interspace mineral soil to 2 cm below the top of the pot. In pinyon and juniper litter treatments the mineral soil was covered with litter to a depth of 2 cm. Litter was a composite of whole and decomposing components. In the buried seed treatment 50 seeds were buried 0.5 cm below the litter or mineral soil surface. Broadcast seeds were placed on the soil or litter surface.

Because previous field seeding trials with the forbs tested here showed spring planting was superior to fall planting in pinyon and juniper woodlands of the Great Basin (Everett 1979), a watering regimen duplicating the short period of spring surface soil moisture was attempted. Seeded pots were watered daily for 2 weeks and then allowed to dry. Seedling emergence was recorded weekly for 4 weeks.

RESULTS AND DISCUSSION

Indigenous Grass Species Trials

Using emergence from interspace mineral soil as a standard the litter fermentation layer appeared to inhibit emergence of all indigenous grass species (fig. 1 A). Emergence was greatest from mineral soil collected under the litter layer for all species. The start of seedling emergence was delayed at least 1 to 6 weeks in tree litter for the species tested. This may reflect a requirement for leaching of allelopathic chemicals before germination. Under field conditions, long leaching periods with a moist soil surface are unlikely during the growing season and reductions in emergence due to allelopathy would be greater than reported here.

Freshly fallen litter used in the second study inhibited seedling emergence of POSA and FEID but not SIHY or BRTE (fig. 1 B). Emergence of BRTE and SIHY was greatest in litter; maximum emergence of POSA and FEID occurred in interspace soils. Again we saw a delay in seedling emergence of POSA and FEID in tree litter. The low BRTE emergence in interspace mineral soil may be the result of the species' sensitivity to soil crusting that did not occur in the previous test. Given a seed source, SIHY and BRTE can readily emerge from litter zones where a fermentation layer is not present.
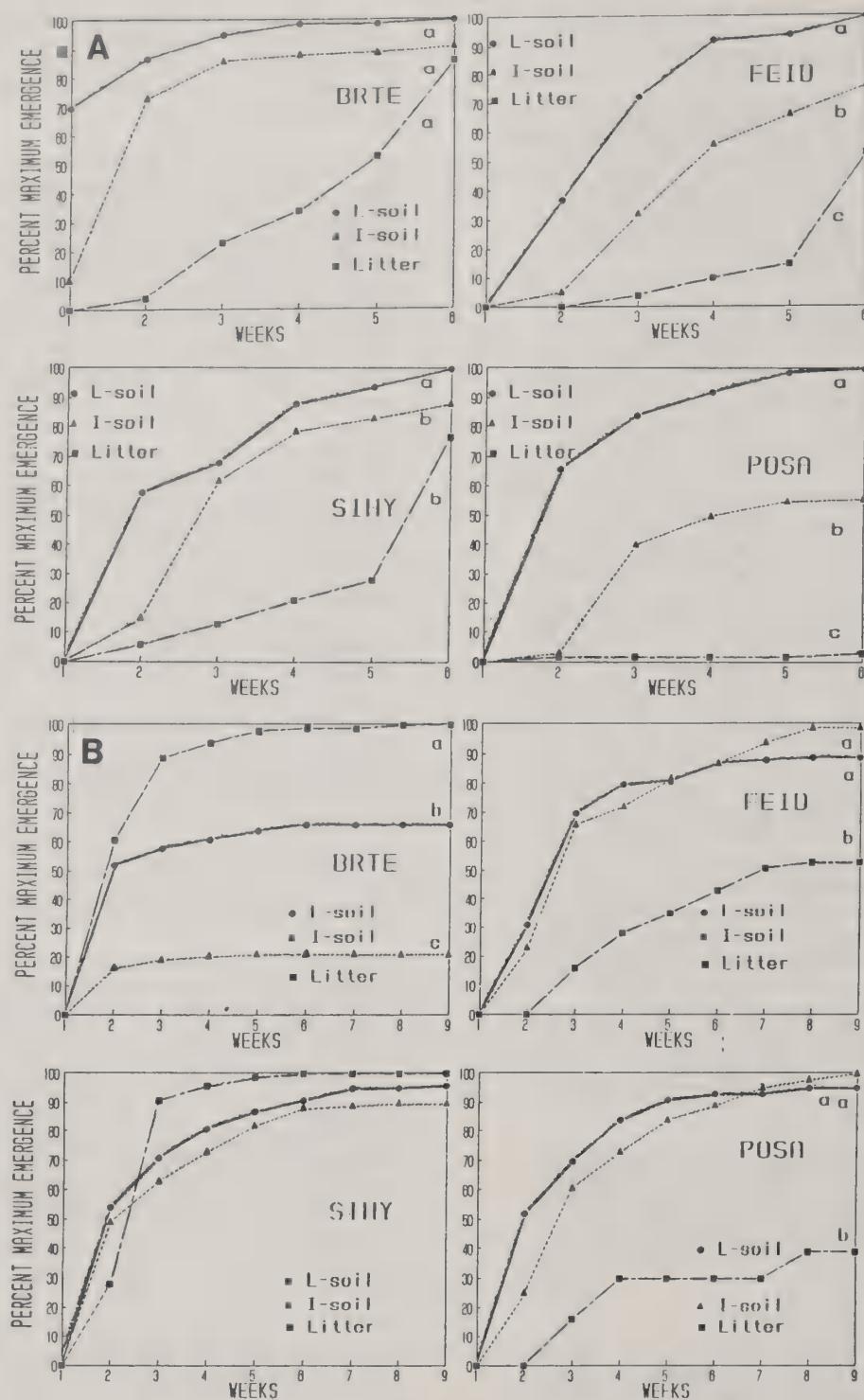
Figure 1. (A) Percent maximum emergence of cheatgrass (BRTE), bottlebrush
squirreltail (SIHY), Idaho fescue (FEID), and Sandberg
bluegrass (POSA) in mineral soil taken from under singleleaf
pinyon litter (L-soil), in mineral soil from the interspace
between trees (I-soil), and in litter from the fermentation
layer of the litter zone. Letters a, b, and c denote
significant (p=0.05) differences in final emergence among
seedbeds for a given species. (B) Loose needle litter
substituted for litter from fermentation layer.

The presence of even loose needle layers inhibits the establishment of POSA and FEID. The exclusion of desirable perennial grasses from tree litter zones following tree harvest leaves a large proportion of the soil surface open to invasion by the undesirable annual grass BRTE.

Emerging seedlings must make contact with mineral soil for adequate growth. Root and shoot weights were greatest for all species in pots filled with mineral soil taken from beneath the litter layer and least for all species in the litter seedbed pots (fig. 2). POSA seedlings did not survive when grown in pinyon litter alone. Root and shoot weights from plants grown in the litter seedbed did not reflect the higher levels of extractable nutrients present (Everett et al. 1986). The weight differences between plants growing in interspace and litter zone mineral soils may be explained by nutrient enrichment in the latter. Pinyon litter appears to limit establishment of indigenous grass species by both reduction in seedling emergence and seedling growth. Perennial species rooted below the litter layer would not be subject to allelopathic effects.
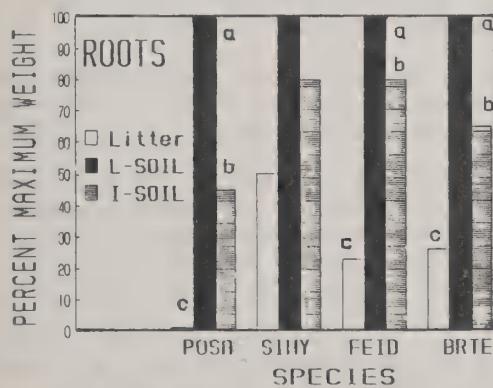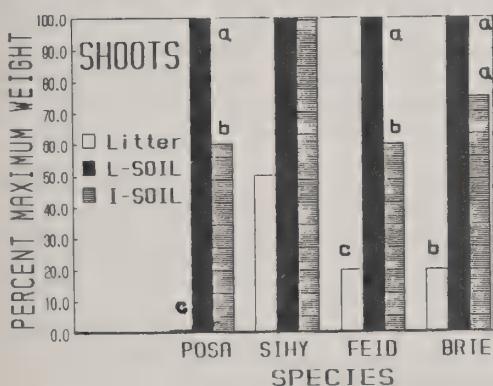
Figure 2. Percent maximum shoot and root weights for BRTE, SIHY, FEID and POSA grown in mineral soil taken from under singleleaf pinyon litter (L-soil), in mineral soil from the interspace between trees (I-soil), and in litter from the fermentation layer of the litter zone. Letters a, b, and c denote significant (p=0.05) differences in shoot and root weights among seed beds for a given species.

Commonly Seeded Species Trials

Buried seeds of AGCR, BRIN, LILE, and MESA were inhibited by the presence of either pinyon or juniper litter (fig. 3). Pinyon litter was more inhibitory than juniper litter for MESA and BRIN seeds but the opposite occurred for LILE. Emergence of buried SAMI seeds showed no response to seedbed type.
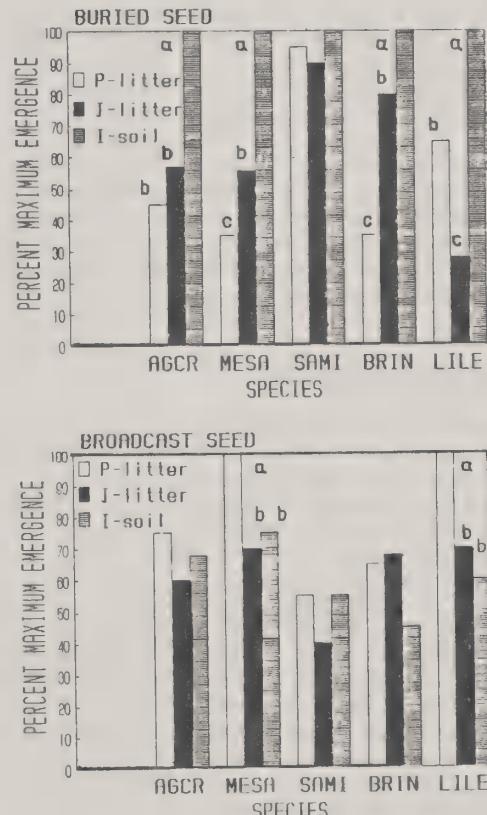
Figure 3. Percent maximum emergence of fairway crested wheatgrass (AGCR), smooth brome (BRIN), 'Ladak' alfalfa (MESA), blue flax (LILE), and small burnet (SAMI) in singleleaf pinyon litter (P), Utah juniper litter (J) and interspace mineral soil (I) from the interspace between trees. Letters a, b, and c denote significant (p=0.05) differences in final emergence among seedbeds for a given species.

There was no significant seedbed effect for broadcast seeds of AGCR, SAMI, and BRIN, but MESA and LILE were stimulated by pinyon litter (fig. 3). In all cases, seedling emergence in pinyon litter was equal to or greater than emergence in interspace soils. Emergence in juniper litter was comparable to that in interspace soils. I speculate that, for broadcast seeds the adverse allelopathic effects of pinyon and juniper litter are more than offset by improved surface microenvironment and reduced seed desiccation. Microtopography provides a degree of protection against seed water loss (Harper et al. 1965)

Emergence from buried seeds was always greater than from broadcast seeds in interspace mineral soil seedbeds. Emergence from broadcast seeds was superior to that from buried seeds in pinyon litter for MESA, LILE, BRIN, and AGCR. Allelopathic effects of litter apparently nullify the advantages of burying seeds. Perhaps germination of seeds is inhibited by the concentration of leachates with litter depth that does not occur at the surface of the litter.

For the short period of needle leaching and moist soil conditions tested here the results suggest seeds should be broadcast on litter seedbeds and buried in interspace microsites. Because of seed desiccation on the soil surface, however, a more practical recommendation would be to seed below the litter layer. Soils beneath the tree litter have been shown to have the greatest seedling emergence and growth for indigenous species. Field seeding trials are required to test seeding techniques suggested by this greenhouse study.

SUMMARY AND CONCLUSIONS

Allelopathy plays an interactive role with other environmental factors in creating understory spatial patterns associated with woodland succession. Results of previous field work and this greenhouse study suggest allelopathy prevents understory establishment rather than eliminating established plants. Differential emergence of indigenous grass species in greenhouse tree litter pots supported field observations of species distribution patterns. Seedling emergence of bottlebrush squirreltail and cheatgrass were least affected by pinyon litter and these species rapidly dominated litter microsites in the field after tree removal. Emergence of Sandberg bluegrass and Idaho fescue was inhibited by pinyon litter; this corresponds to field observations.

The presence of singleleaf pinyon or Utah juniper litter can be a negative factor in seedling emergence if seed is buried. Probably allelopathy is secondary to drought stress in limiting emergence. Tree litter apparently improves moisture status of broadcast seed subjected to desiccation.

The level of allelopathic chemical activity in the litter of singleleaf pinyon and Utah juniper is not found in the mineral soil below. Although past research has shown allelopathic compounds are easily leached from juniper and pinyon litter in the laboratory, these chemicals either not leached in situ or are inactive in the mineral soil. Seed emergence and growth is greater in mineral soil under tree litter than in mineral soil from the interspace between trees.

Seedling emergence from tree litter should be a considered in selecting species for seeding cut-over woodlands. Because more than 50 percent of the ground surface can be occupied by tree litter, attention to seedbed effects is required.

If seeds are drilled, then seed must be placed below the litter layer. If seeds are broadcast, species should be selected for their ability to establish in the tree litter. MESA, LILE, and AGCR had high seedling emergence when broadcast onto pinyon litter.

LITERATURE CITED

Anderson, R. C., O. L. Loucks, and A. M. Swain. 1969. Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. Ecol. 50:255-263.

Arnold, J. F. 1964. Zonation of understory around a juniper tree. J. Range Manage. 17:41-42.

Everett, R. L. 1979. Emergence and survival of seeded shrubs and forbs. Abstract. 31st Ann. Meeting. Soc. Range Manage. Casper, Wy.

Everett, R. L. and S. D. Koniak. 1981. Understory vegetation in fully stocked pinyon-juniper stands. Great Basin Nat. 41:467-476.

Everett, R. L. and S. H. Sharrow. 1983. Understory seed rain on tree-harvested and unharvested pinyon-juniper sites. J. Environ. Manage. 17:349-358.

Everett, R. L. and S. H. Sharrow. 1984. Response of grass species to tree harvesting in singleleaf pinyon-Utah juniper stands. USDA Forest Service, Intermountain Forest and Range Exp. Sta. Ogden, Ut. Res. Pap. INT-334. 7 p.

Everett, R. L. and S. H. Sharrow. 1985. Soil water and temperature in harvested and nonharvested pinyon-juniper stands. USDA Forest Service. Intermountain Res. Sta., Ogden, Ut. Res. Pap. INT-342. 5p.

Everett, R. L. and K. Ward. 1984. Early plant succession on pinyon-juniper controlled burns. Northwest Sci. 58:57-68.

Everett, R. L., S. H. Sharrow, and R. O. Meeuwig. 1984. Pinyon-juniper woodland understory distribution patterns and species associations. Torrey Bot. Club Bull. 110:454-464.

Everett, R. L., S. Sharrow, and D. Thran. 1986. Soil nutrient distribution under and adjacent to singleleaf pinyon crowns. Soil Sci. Soc. Amer. J. 50:788-792.

Harper, J. L. 1977. The population biology of plants. Academic Press, London. 892 p.

Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. The behaviour of seed in soil: The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. of Ecol. 53:273-286.

Jameson, D. A. 1961. Growth inhibitors in native plants in northern Arizona. USDA Forest Service. Rocky Mountain Forest and Range Expt. Sta. Fort Collins, Co. Res. Note RM-61: 2 p.

Jameson, D. A. 1966. Pinyon-juniper litter reduces growth of blue grama. J. Range Manage. 20:247-249.

Johnsen, T. N. 1962 One-seed juniper invasion of northern Arizona grasslands. Ecol. Monogr. 32:187-207.

Lavin, F., D. A., Jameson, and F. B. Gomm. 1968. Juniper extract and deficient aeration effects on germination of six range species. J. Range Manage. 21:262-263.

Rice, E. L. 1974. Allelopathy. Academic Press, New York. 353 p.

Snedecor, E. W. and W. G. Cochran. 1978. Statistical Methods. Iowa State University Press, Ames. 593 p.

SEEDBED SALINITY AND THE ESTABLISHMENT OF RANGE
PLANTS

Bruce A. Roundy[1]

ABSTRACT

Many rangelands throughout the world have salt-
affected soils. Establishment requirements may
be complex, but must be understood for successful
revegetation of these soils. The potential to
select or breed for specific characteristics from
an abundance of salt-tolerant plant materials
offers good possibilities for establishing forage
plants adapted to specific sites.

OCCURRENCE OF SALINE RANGELANDS

Salt-affected soils cover 7 percent of the world's
land area (Dudal and Purnell 1986). Much of these
lands are used for forage or fuelwood production
since they are too arid or saline for intensive
agriculture.

Geological history and physiography, climate and
agricultural practices may all act or interact to
produce salt-affected soils. Marine sediments from
ancient seas commonly are the source of saline
surface or subsurface layers such as in the Northern
and Central Great Plains of North America (McKell
et al. 1986). In arid or semiarid areas throughout
the world, salts from marine deposits and from
natural weathering processes accumulate in lowlands
due to restricted drainage and lack of leaching
(Chapman 1975). High water tables produced along
natural floodplains and in naturally closed basins
such as in the Great Basin of North America deposit
salts in surface soils, especially where evaporation
is high. Lack of drainage and insufficient
leaching has resulted in salination of many
irrigated lands throughout the world (Carter 1975).
Many of these lands are subsequently used as
rangelands or abandoned altogether. In the Great
Plains of North America and in Australia, land
clearing and cultivation has created saline seep
problems by decreasing evapotranspiration,
resulting in localized raising of the water table
through saline subsurface layers (Bettenay 1986,
McKell et al. 1986). Erosion of topsoil associated
with cultivation may expose saline subsoils
resulting in bare to sparsely vegetated areas known
as "scalds" in Australia (Bettenay 1986). Mining
operations may expose sodic overburdens such as
the palocene shales in North Dakota and the
cretaceous shales in New Mexico (Gee et al. 1978)
or produce saline waste material such as retorted
oil shale (Schmehl and McCaslin 1973). Plant
community disturbances that result in dominance by
plants such as Halogeton glomeratus (C.A. Mey) or
Sarcobatus vermiculatus (Hook.) Torr. may result in
soil salinization as ions are leached from plant
parts (Eckert and Kinsinger 1960, Rickard 1965).

---

[1]Assistant Professor, Range Management, School of
Renewable Natural Resources, University of Arizona,
Tucson, AZ 85721.

Whether due to natural or artificial salination,
rangelands with salt-affected soils are a world-wide
occurrence. Since optimum use of these rangelands
will depend on their dominance by beneficial forage
and fuelwood plants, an understanding of natural
and artificial establishment of these plants is
essential.

SALT-AFFECTED SOILS

Salt-affected soils are generally classified
according to the amount of soluble salts in the
saturation extract as measured by the electrical
conductivity (ECe) and the percentage of the
exchange complex occupied by sodium (exchangeable
sodium percentage-ESP) (Table 1). Saline soils
are those that have a high concentration of soluble
salts that lower the osmotic potential of the soil
solution and that may be toxic to seeds or plants.
Sodic soils have a high concentration of sodium
on the soil exchange complex, but a low
concentration of total salts. Fine-textured soils
with expanding clays such as montmorillonite easily
disperse at even moderate ESP's, have low
infiltration rates and hydraulic conductivity when
wet and develop a hard crust when dry. In addition
to the negative effects of sodium on plant growth
caused by physical deterioration of the soil, high
concentrations of sodium ions may also cause
nutritional imbalances that interfere with
germination and growth (Maas 1986). Soil structure
and hydraulic conductivity is maintained in saline
sodic soils by a high concentration of divalent
ions in addition to sodium. These soils may limit
plant growth by low osmotic potential or ion
toxicity but not by soil physical deterioration
unless the nonsodium ions are leached out.

Table 1. Classification of saline soils

U.S. Salinity Lab[1]	ECe (dS·m^{-1})	ESP %
Saline	> 4	< 15
Saline-sodic	> 4	> 15
Sodic	< 4	> 15

FAO/UNESCO[2]

Solonchak	15 upper 0.75-1.25m	
Saline phase	4-15 upper 1.0m	
Solonetz		> 15 upper 0.4m
Sodic phase		6-15 upper 1.0m

---

[1]U.S. Salinity Lab (1954)

[2]Food and Agriculture Organization of the United
Nations/United Nations Educational Scientific
and Cultural Organization, reported in Dudal and
Purnell (1986).

The main soluble salts in salt-affected soils consist of Ca^{2+}, Mg^{2+} and Na^+ cations and SO_4^{2-} and Cl^- anions with smaller quantities of K^+, HCO_3^-, CO_3^{2+} and NO_3^- (Sandoval and Gould 1978). Predominant ions in saline soils in Australia are Na^+ and Cl^- of marine origin and deposited by rainfall (Nulsen 1986). Major ions of the northern Great Plains are Na^+, Mg^{2+} and SO_4^{2-} (Nulsen 1986). In the Great Basin, Na^+, K^+, Cl^- and SO_4^{2-} are generally more dominant than Ca^{2+} or Mg^{2+} (Roundy 1984). Some Great Basin playas have accumulated boron from hot springs which become boron-enriched from late-stage differentials of granitic magmas (Papke 1976). Sediments high in boron are then eroded from playa surfaces and deposited by wind on adjacent soils (Young and Evans 1986). Though an essential micronutrient, boron may occur at concentrations high enough to limit growth of range plants on some saline soils (Roundy 1985b).

The two main factors over which there is some control in establishing plants on saline rangelands are the seedbed environment and the plant materials chosen for establishment. The environment to which seeds and seedlings are exposed may be influenced by the season, method and cultural practices associated with revegetation. The response of the plant materials used to the environmental conditions of the seedbed will determine establishment success. For these reasons, understanding establishment of range plants on saline seedbeds is dependent on understanding the dynamics of the seedbed environment and the adaptations of plants to avoid or tolerate associated environmental stresses.

The main effect of soluble salts on plants is that of decreasing water availability (Bernstein 1961). Each increase in salinity, measured by an increase in electrical conductivity of $1dS \cdot m^{-1}$, will decrease the osmotic potential of the soil solution approximately 0.036 MPa (Campbell et al. 1948, U.S. Salinity Lab 1954) depending on the activity, solubility and tendency to form ion pairs of the particular ions in solution. In soils where highly soluble salts such as NaCl and Na_2SO_4 are dominant, increasing salt concentration at high water contents or decreasing water content of even moderately saline soil, greatly reduces the solution osmotic potential (Roundy 1984, fig. 1). On arid and semiarid rangelands, salinity interacts with temperature and precipitation in affecting germination and growth responses. Plants and seeds in salt desert environments are subject to short periods when temperature and soil water potential are favorable for growth (Caldwell 1974).

Soil osmotic potential varies not only with seasonal changes in soil water content but also with changes in soil salinity in response to precipitation and evaporation. Salts may be leached from the seedbed by seasonal precipitation (Teakle and Burvill 1938, Zallar and Mitchell 1970, Rajpurohit and Sen 1980). Depth of saline or sodic layers in the soil may correspond closely with the depth of water penetration (Eisenberg et al. 1982). Surface soils may increase
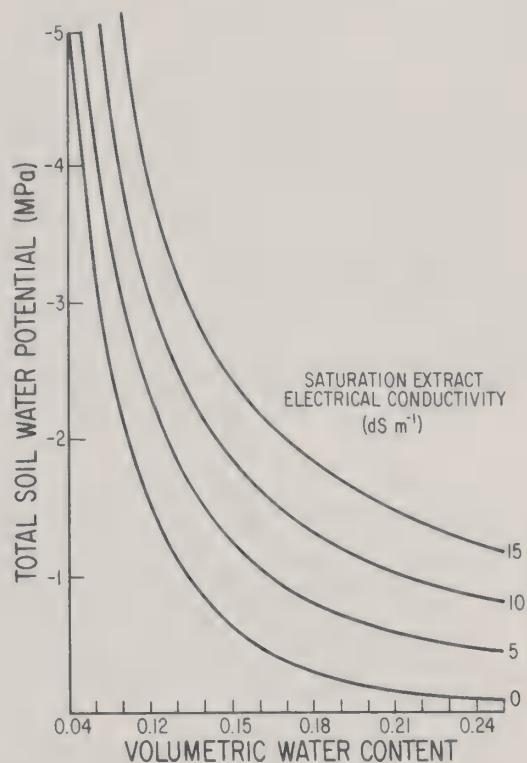
Figure 1. Total soil water potential in relation to volumetric water content and salinity for a silt-loam soil on salt-desert shrub rangeland in Nevada (after Roundy 1984).

greatly in salinity after a wet season during evaporative periods as the water table rises and deposits salts near the surface (Jackson et al. 1956). Even on soils where the water table is not raised high enough to interact with the soil surface, seedbed salinity may increase following the wet season as evaporation and capillary rise carry salts previously leached to the subsoil back to the surface (Roundy et al. 1984). Wind may erode the surface salts of playas (Young and Evans 1986) or adjacent soils (Roundy et al. 1984) in the Great Basin. These salts are deposited on upland alluvial fans (Young and Evans 1986) but may eventually be washed back down to the playa in overland or subsurface drainage as part of a large salt cycle (Roundy and Young 1985). Natural distribution of plants in the salt desert is related to depth, fluctuations and salinity of the water table, and salinity, texture, structure, surface morphology, and water relations of the seedbed in relation to plant tolerances and requirements (Roundy and Young 1985, Young et al. 1986).

The seedbed environment in saline deserts may range from cool and saturated to hot and dry, with salinity varying from low to high (McKell 1986). Soil water, salinity and temperature are all highly dynamic in the seedbed and greatly

affect germination and seedling establishment.

GERMINATION IN SALINE SEEDBEDS

Germination in saline seedbeds may be most limited by low soil matric and osmotic potentials or by toxic concentrations of specific ions. Seeds of different species have different hydration levels below which the physiological processes of germination are slowed or prevented (Koller and Hadas 1982). This direct effect of water potential on germination can be determined by observing germination responses in solutions with osmotic potentials reduced by adding organic polymers of high molecular weight which do not enter the seed, such as polyethylene glycol (PEG) 6000 (Sharma 1973). Germination in drying soil at low matric potentials is also limited by reduced water entry into the seed, as water is left in only the smaller pores and seed-soil-water contact is reduced (Hadas and Russo 1974a, 1974b). Soil hydraulic conductivity is generally much higher than seed water conductivity and is probably not directly limiting to seed water uptake (Koller and Hadas 1982). However, if evaporative demand in the seedbed exceeds subsoil hydraulic conductivity, the seedbed rapidly dries out.

The osmotic potential of saline soils is not necessarily additive to the soil matric potential in limiting water uptake. Ions may enter the seed, lowering its osmotic potential and facilitating hydration (Sharma 1973). Seeds permeable to ions in a highly saline but saturated seedbed could be well-hydrated even though the soil osmotic potential might be very low. The extent to which this favorable effect of increased hydration due to entering ions is equally or dominantly offset by ion interference with germination processes varies with the species and salts (Ungar 1978). This phenomenon can be tested by comparing germination in PEG with germination in different salts at the same osmotic potentials (Young et al. 1983). Sensitivity at germination to different ions such as Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-} varies among different plant materials (Rauser and Crowle 1963, Hyder and Yasmin 1972, Redmann 1974, Ryan et al. 1975, Roundy et al. 1985). Total germination of many species is more affected by osmotic potential than the specific salts in solution (Rauser and Crowle 1963, Ungar and Capilupo 1969, Ungar and Hogan 1970, Macke and Ungar 1971) but germination rate and radical growth may be decreased more by specific ions than total germination (Roundy et al. 1985).

Ability to germinate at high salt concentrations or at low osmotic potentials may be important for establishment of some plants on saline soils but is not necessarily essential. Some halophytes are able to germinate at much higher salinities than most glycophytes and many other halophytes (Ungar 1974, Clarke and West 1969). But most halophytes germinate well in distilled water and many are unable to germinate at as low an osmotic potential as many glycophytes (Ungar 1978). Chapman (1975) suggested that natural reductions in surface salinity were necessary for germination in saline areas. Natural emergence of some halophytes has been observed to only occur during winter and springtime when precipitation is high and salinity stress is reduced (Ungar 1978). Since much more water is required for growth than for germination, regulatory mechanisms help delay germination until soil moisture conditions are conducive to seeding survival in water-limited seedbeds (Koller and Hadas 1982).

Because arid, saline seedbeds have erratic and highly variable periods of moisture availability (Roundy et al. 1984), natural halophytes in these environments have a number of different germination strategies. Species of the Chenopodiaceae family, which are important forage plants on saline rangelands worldwide, provide good examples of these strategies (Young et al. 1984). Many annual species such as Halogeton glomeratus, (M. Bieb) C.A. Mey and Chenopodium album L. have polymorphic seeds, some of which uncoil their embryos and develop root hairs in a matter of hours when exposed to water. Other seeds on the same plant may be long-lived and break dormancy only under specific moisture and temperature conditions. Larger seeds of Atriplex triangularis Willd. are less sensitive to temperature and salinity than smaller seeds (Khan and Ungar 1984). The larger seeds germinate early in the spring while most of the smaller seeds remain dormant providing a long-term seed bank. In some species, indurate fruiting bracts induce dormancy by limiting water flow to the embryo by creating a physical barrier or by releasing salts shunted to them during growth that lower the osmotic potential around the seed. These bracts may also contain high concentrations of organic chemicals (Nord and Van Alta 1960) or ions such as chloride (Wood 1925, Beadle 1952, Twitchell 1955) which inhibit germination. All of these factors may control germination of different collections of Atriplex canescens (Pursh) Nutt. seed (Young et al. 1984).

An important characteristic of seeds of halophytes compared to those of glycophytes is their ability to remain viable for long periods at low osmotic potentials and germinate rapidly with increasing water potential (Ungar 1978). This supports the idea that germination at low osmotic potentials may be nonadaptive for natural establishment in some saline seedbeds. Young and Evans (1981) found an inverse relationship between the germination of basin wildrye [Leymus cinereus (Scribn & Merr.) A. Love] seeds at low osmotic potentials and the salinity of the surface soil of the native stands which produced the seeds.

Seeds in saline seedbeds which fail to germinate under low osmotic potentials may undergo natural "priming" or osmotic preconditioning (Strogonov 1962) which allows rapid germination when water availability increases. Artificial priming of seeds is the practice of soaking seeds at controlled water potentials and temperatures to allow germination processes to begin but not to allow radical emergence (Koller and Hadas 1982). The phenomenon of priming has been known for some time (Levitt and Hamm 1943) but recently has received much attention in the treatment of crop seeds

(Heydecker and Coolbear 1977). Responses to priming include increased rate of germination, increased uniformity of germination for a population of seeds, increased germination and growth of seedlings at low temperatures and increased yield of established plants (Khan et al. 1980/81). Control of seed water potential is usually done by soaking seeds in osmotic solutions of PEG or salts and is referred to as osmoconditioning. Different operational levels of hydration for germination processes that occur during the transition phase of germination, after initial imbibition and before growth, are probably the basis for responses to osmoconditioning (Koller and Hadas 1982). Circumstantial evidence previously mentioned (Ungar 1978) indicates that natural osmoconditioning may be important to germination in saline seedbeds.

Priming by means in addition to, or other than, low osmotic potentials may also occur in nature (Koller and Hadas 1982). Seeds may remain in the transition phase of germination until suitable conditions of such factors as temperature or light stimulate the elimination of an inhibitory factor or the activation of an essential factor and growth begins (Koller and Hadas 1982). Germination of many seeds can be primed and accelerated by cycles of hydration and dehydration (Hegarty 1978). Of course, different species vary greatly in their germination responses to the duration and amount of hydration, dehydration and rehydration.

Ability of seeds to initiate but not complete germination processes at low water potentials, low temperatures or during short periods of hydration may be considered adaptive for natural seedling establishment similar to the adaptive function of dormancy mechanisms (Hegarty 1978).

Osmotic inhibition of germination, either by salts or PEG, has been shown to be less at low than high temperatures for a number of species (Springfield 1966, Odegbaro and Smith 1969, Francois and Goodin 1972, Sharma 1976, Potter et al. 1986). Cold pretreatments may remove dormancy of some species, such as Atriplex hastata L. (Ward 1967). The ability to germinate at low osmotic potentials and low temperatures may be important to establishment of plants on saline soils of cold deserts where precipitation occurs in the winter and seedbed water potentials quickly decrease as temperatures increase in the spring.

Highest germination of saltgrass [Distichlis spicata var. stricta (Torr.) Beetle] occurs at diurnal temperature fluctuations of 20°C and an osmotic potential of -0.1MPa, (Cluff et al. 1983). These temperature and moisture conditions would rarely overlap in natural seedbeds. Some germination of saltgrass occurs at low temperatures and low to high osmotic potentials representative of conditions in a natural saltgrass seedbed in March (Cluff and Roundy[2]). These observations

suggest that natural germination of saltgrass in saline seedbeds may occur only in early spring when the seedbed is cool but wet, or in the spring and summer where the soil is saturated by a standing body of water such as near a marsh or by unusually high precipitation (Cluff and Roundy[2]). This may be the case with natural establishment of other plants on saline, arid rangelands. Possibly only a few seeds germinate under the normal suboptimal moisture and temperature conditions. But if precipitation is unusually high or prolonged, large numbers of seeds may germinate, some of them being naturally primed by osmoconditioning and cycles of hydration and dehydration. Noy-Meir (1973) has observed that high seedling establishment in deserts may occur only sporadically in response to a culmination of highly favorable moisture events.

Soil physical conditions and microtopography may greatly influence seedling emergence on saline rangelands. The lack of aggregate stability associated with low organic matter, high concentrations of sodium, and fine particle size distribution encourages crust formation on many salt-affected soils (Miller and Gifford 1974). Soil crusts limit infiltration and restrict seedling emergence. Low soil osmotic potentials reduce the ability of seedlings to penetrate soil crusts (Frelich et al. 1973). Penetrability of soil crusts increases greatly with wetting but rapidly decreases as the soil dries out (Roundy et al. 1984). Soil surface cracks may be important safe sites (Harper 1977) for emergence of seedlings from crusted saline or nonsaline soils (Roundy et al. 1984, Eckert et al. 1986).

Studies determining the germination responses to important environmental variables such as osmotic potential, water potential, ion concentrations and temperature have been most numerous and are important in understanding establishment of plants on saline rangelands. Additional studies of this kind are necessary for many other range plant materials. Information on germination responses to osmoconditioning and hydration-dehydration treatments is available for a few crop plants (Heydecker and Coolbear 1977) but is limited for range plants. Lack of knowledge of the ecological significance of these responses limits our understanding of the germination ecology of saline and arid rangelands. As noted by Young et al. (1984), data for the physical parameters of field seedbeds is vital and is needed to determine the ecological significance of biological responses. Also needed are more studies similar to that of Khan and Ungar (1984) which attempt to determine the ecological significance of seed polymorphism. Methodology developed in these studies may be helpful in determining the significance of more subtle germiantion control mechanisms.

SEEDLING ESTABLISHMENT

Seedling establishment is generally more sensitive to environmental stresses than germination of seeds (Osmond et al. 1980). Since germination and seedling or mature plant tolerance to salinity

71

and low soil osmotic potentials may not be correlated for a particular plant material, (McGinnies 1960, Manohar et al. 1968, Sharma 1973) germination, plant growth and survival studies are all necessary to determine environmental limitations to establishment.

On saline, arid soils matric and osmotic potentials may decrease and soil solution salt content increase rapidly as the soil dries out (Roundy et al. 1984). Of course, soil drying time is a function of evaporative demand and will be much slower after winter than summer storms. Osmond et al. (1980) citing Cowling (1969) reported drying times to a soil water potential of -1.5MPa of less than one day and 4.5 days for the 0-5 cm and 5-10 cm depth intervals, respectively, after a summer rain on a clay-loam soil in Australia. In the winter, the 0-5 cm interval took 1.5 days and the 5-10 cm interval took 10 days to reach -1.5MPa soil water potential. In Nevada, a moderately saline soil (ECe = 7.0 dS·m^{-1}) averaged 0.2 to 0.6 MPa lower total soil water potential in the 10-15 cm depth interval than a nearby nonsaline soil as the soils dried out in the spring and summer (Roundy et al. 1984). This lower total water potential was due to the lower osmotic potential of the saline soil. Survival of seedlings on these saline, arid soils is probably dependent on maintaining root elongation to stay below the soil drying front.

Soil salinity may negatively affect plant growth by reduction of water availability by specific ion interference with physiological processes, or by creation of nutritional imbalances (Magistad 1945, Hayward and Wadleigh 1949, Epstein 1972, Bresler et al. 1982). Bernstein (1964) has argued against the importance of reduced water availability or "physiological drought" due to salinity, suggesting that most plants adjust osmotically to maintain water uptake and turgor. To adjust osmotically, plants must absorb and accumulate solutes or synthesize them. Additional reviews of osmotic adjustment, turgor maintenance (Hsiao et al. 1976, Turner and Jones 1980) and salinity tolerance (Poljakoff-Mayber and Gale 1975) support the idea that plant growth under low soil osmotic potentials is dependent on osmotic adjustment to maintain turgor necessary for cell elongation. However, plants growing in saline soil may have greatly reduced growth even though positive turgor is maintained by osmotic adjustment (Roundy 1983, 1985c). The capacity to tolerate or exclude specific ions and still adjust osmotically to maintain a favorable water balance may be the essence of salt tolerance.

The most common cause of specific ion effects is that of sodium and its induction of calcium deficiency (Ratner 1935, Hayward and Wadleigh 1949, Magistad 1945). However, plants may vary greatly in their sensitivity to sodium and other ions. All ions predominantly found in saline soils may have specific negative effects (Levitt 1980, Bresler et al. 1982). Soil nutrients such as N and P may increase or decrease salt tolerance of different plants (Bresler et al. 1982).

Many range plants are more tolerant of boron than agricultural crops. Cold desert halophytes evidently tolerate, rather than exclude, boron (Caldwell 1985). Germination may be less sensitive to boron than seedling growth (Roundy 1985b) and halophytes may vary in their growth responses to high boron concentrations (Breckle 1975 cited in Caldwell 1985). Boron concentrations may vary greatly in the seedbed (Roundy 1985b) and their effect on growth and, in turn, on establishment and competition are uncertain (Caldwell 1985). As emphasized in Boyko (1966), most plants are more tolerant of balanced salt solutions than solutions of single salts. Thus, determination of growth responses to salinity for ecological interpretations should be done using solutions of generally similar chemical composition as field soil solutions.

Rapid seedling root elongation as tested in the laboratory may not always directly correspond with observed ease of seedling establishment in the field (Simanton and Jordan 1986). However, where periods of available water are limited, it is reasonable to expect greater establishment from seedlings with root growth that is rapid enough to stay ahead of the soil drying front. This, of course, assumes availability of soil water in the subsoil.

Radical growth of tall wheatgrass (Elytrigia pontica (Podp.) Holub Syn: Agropyron elongatum (Host) Beauv.) was greater at high and low osmotic potentials (Roundy et al. 1985), and root elongation was greater in unsalinized and salinized soil (Roundy 1985c) than basin wildrye. These laboratory responses corresponded to greater establishment and survival of tall wheatgrass than basin wildrye on a nonsaline and on a saline soil in the field (Roundy 1985a). Tall wheatgrass also reduced the soil water potential much lower than basin wildrye in nonsaline and salinized soil columns in the growth chamber before growth cessation (Roundy 1985c). The ability of tall wheatgrass to rapidly grow an extensive root system in nonsaline or moderately saline soil is evidently an important establishment characteristic. Jensen (1982) found that salination of barley (Hordeum vulgare L.) before a drying cycle resulted in slower soil desiccation and an extended growth period but no differences in yields, transpiration coefficients, or wilting percentages compared to unsalinized plants. He suggested that the delay in water uptake due to salinity may be advantageous when water is limited by intermittent periods of drought. Reduced water use due to lack of growth associated with soil salinity may delay desiccation for a time, but the value of this to survival is dependent on eventually receiving precipitation before evaporation dries out the soil anyway. Also, failure of desirable species to use the soil water may allow invasion by undesirable and competitive weedy species.

The root elongation of seedlings may vary greatly with respect to soil salinity and texture and its importance to survival can only really be assessed in relation to precipitation patterns and soil

water holding capacity. Osmond et al. (1980) have reported work by Williams (1972) which sought to determine the importance of plant establishment on the maintenance of pure stands of Atriplex vesicaria Heward ex Benth. and Maireana pyramidata (Benth.) Paul G. Wilson on adjacent but different soils in Australia. Osmond et al. (1980) suggested that the greater root elongation of Maireana on its native sandy loam soil than Atriplex may allow it to establish when Atriplex can not, when precipitation is infrequent and the soil rapidly dries out due to its low waterholding capacity. Atriplex, however, establishes better and dominates the clay soil perhaps because of its greater root elongation than Maireana on that soil. This study, which compared germination and establishment in relation to precipitation and soil type, suggests that factors affecting seedling survival may be a greater determinant of establishment than those affecting germination. Additional studies of this type, which determine the relationship of biological responses such as root growth to environmental variables, including soil water dynamics, soil physical characteristics and salinity, are necessary to understand seedbed ecology of saline soils.

SPECIES SELECTION

Selection of adapted and useful plant materials is probably the greatest challenge, but also the most potentially successful decision-making that can be done in revegetating saline, arid rangelands. Extensive field trials and ecological studies provide the basis for species recommendations throughout the world. Some recent literature includes reviews of salt tolerant plants for fuelwood (Midgley et al. 1986), for summer rainfall areas (Fisher and Skerman 1986), for the Mediterranean Basin (Lehouerou 1986) for arid areas in the Near East and North Africa (El Hamrouni 1986, Kernick 1986), and for Australia (Runciman 1986). Because of their extensive distribution on nonsaline and saline deserts throughout the world, members of the Chenopodiaceae family and especially of the genus Atriplex, have been studied intensively to understand their unique adaptability, and also extensively to determine potential for revegetation (Jones 1970, Osmond et al. 1980, and Tiedemann et al. 1984). Workers at the U.S. Salinity Laboratory have compiled an extensive bibliography of plant responses to salinity (Francois and Maas 1978, 1985) and have indexed the salt tolerance of many crops and forage species (Maas and Hoffman 1977, Maas 1986). Numerous salt-tolerant plant materials are available and considerable literature has been published about many of these materials.

In addition to a knowledge of salt-tolerance, selection of plant materials for saline rangelands must also be guided by a knowledge of tolerance to other environmental stresses such as drought, extreme temperatures and poor soil aeration. Due to subtleties of plant adaptation to specific environments, extensive testing is necessary to develop sound plant materials recommendations.

Atriplex canescens (Pursh.) is the most popular Atriplex for reseeding in the United States (Carlson 1984). Yet, use of nonlocal seed sources has resulted in failure, prompting development of regionally adapted cultivars (Carlson 1984).

Long-term persistence in relation to environmental stresses and management practices are also necessary information when planning revegetation. Because tall wheatgrass is more salt and drought tolerant than basin wildrye at germination and at the seedling stage, it was more easily established on a saline soil in the Great Basin (Roundy 1985a). However, tall wheatgrass may not persist on dry saline soils receiving less than 300 mm annual precipitation, to which basin wildrye is adapted. More information is needed on the persistence of salt tolerant species, as a function of their ability to compete and reproduce in different environments.

Although naturally-occurring species may be considered best adapted, some produce little seed for revegetation projects and may have complex, unknown requirements for establishment, including involvement of mycorrhizae and N-fixing organisms (Jefferies and Pitman 1986). Information on growth of most halophytes is limited (Hoffman and Shannon 1986), as is that on suitability and proper management of many of these plants as forage (Jefferies and Pitman 1986, Leigh 1986). Atriplex sembaccata R. Br., for example, is easily established and has high production, but is sensitive to grazing (Leigh 1986). Norton (1986) has rejected the use of animal-based models for determining stocking rates on saline shrublands, emphasizing the variable precipitation and forage production on these lands. He also emphasized the importance of vegetation monitoring to guide management to ensure persistence of natural stands or expensive revegetation projects. Development of comprehensive information on establishment, persistance and management of the numerous plant materials presently available offers great potential for revegetation of saline rangelands.

IMPROVED PLANT MATERIALS

Many species have a wide variability in salt tolerance and thus a high potential for selection for salt-tolerant genotypes. Some of these species do not naturally occur on saline land, possibly due to lack of adaptation to some other environmental conditions (Ashraf et al. 1986).

Some chenopod shrubs, especially the Atriplexes, have high potential for cultivar development due to high natural variation, interspecific hybridization and polyploidy (Carlson 1984). Superior Atriplex strains are being identified and interspecific hybrids developed which will be important for revegetation of nonsaline and saline arid lands (Stutz and Carlson 1985). These authors suggest that selections should be genetically rich to be the most adapted to the heterogeneous environments of rangelands. Dewey (1960, 1962) found sufficient genetic variation among Agropyron strains to allow a plant breeding program. Such

a program could yield very useful forage plants for areas which are too saline for drought-tolerant plants or too dry for salt-tolerant plants now available (Young and Evans 1981).

Improved cultivars of Russian and Altai wildrye (Psathrostachys juncea (Fisch.) Nevski Syn: Elymus junceus Fisch. and Leymus angustus (Trin.) Tzuelev Syn: Elymus angustus Trin.), as well as interspecific hybrids such as quackgrass (Elytrigia repens (L.) Nevski Syn: Agropyron repens (L.) Beauv.) x bluebunch wheatgrass (Pseudoroegneria spicata (Pursh) Love Syn: Agropyron spicatum (Pursh) Scribn. & Smith) offer promise for seeding saline rangelands in cold deserts (Asay and Knowles 1985). McKell (1986) predicted that salt and stress tolerant varieties from somaclonal variants surviving high stress culture solutions will soon be available.

Shannon (1980) has reviewed information on the genetics of salt tolerance. Moderate salinity does not alter the physiological and biochemical processes of growing cells, and basic biochemical differences between halophytes and glycophytes are not apparent. However, in salt-stressed plants, specific metabolites are reduced as growth rate decreases, and plant development, though unaltered, is slowed. The decrease in growth of salt-stressed plants may be due to diversion of metabolic energy from growth processes to osmotic and ionic processes of normal cellular maintenance (Nieman and Maas 1978 cited by Shannon 1980). In glycophytes, ion exclusion is associated with salt tolerance, but ion exclusion fails under high salinities. Although substantial research has not yet produced precise understanding of the mechanisms of salt tolerance, it has laid the foundation for genetic research by finding sufficient variation among interfertile genotypes, by developing salt tolerance measurements and by discovering the correlation of salt tolerance and genetically-controlled ion transport processes. Shannon's observations regarding genetic fitness to salinity, as expressed by reproductive, absolute growth, and survival responses, rather than just relative growth, are especially revelevant to breeding programs for salt tolerant range plants.

Malcolm (1986) considered it unlikely that extreme salt tolerance could be bred into glycophytes. He argued that the use of halophytes as forage is a more economically acceptable use of highly saline lands.

The salt tolerance of many halophytes is no doubt associated with their ability to osmotically adjust (Poljakoff-Mayber and Gale 1975) but excrete excess ions through trichomes or salt glands (Mazafar and Goodin 1970, Thomson 1975, and Hansen et al. 1976). Other halophytes dilute accumulated ions by increasing succulence (Caldwell 1974). Selecting or breeding for desirable establishment or forage characteristics in natural halophytes may offer possibilities for improved plant materials for saline rangelands.

Refinement of species recommendations and development of improved plant materials for revegetation of saline rangelands is apparently limited by the scope and amount of development and evaluation research, not by biological potential.

ESTABLISHMENT TECHNIQUES

Direct seeding, when possible, is the least expensive and most desirable method of revegetating rangelands. However, direct seeding of saline, arid rangelands has had limited success (Bleak et al. 1965, Plummer 1966, Malcolm 1972, Eckert et al. 1973, Roundy 1985a). Failures have been attributed to inadequate precipitation, intolerance of plant materials to drought and salinity, and unfavorable interactions of moisture and temperature on germination and survival. Direct seeding is not recommended for sites receiving less that 250 mm annual precipitation (McKell 1986).

Seedbed preparation techniques have been developed to favorably modify the soil water, salinity, and temperature conditions of the seedbed to successfully seed some sites. Seeding into furrows increases soil water availability for germination and growth (McGinnies 1959, Evans et al. 1970). Furrowing may concentrate soil water near the seedling and reduce evaporative water loss by reducing soil and air temperatures (Evans et al. 1970). Furrowing may also promote leaching of salts by natural rainfall (Fanning and Carter 1963). Deep-furrow seeding may increase seedling establishment on semiarid sites compared to standard furrows, except on highly unstable vesicular-crusted soils (Wood et al. 1982). On these unstable silt loam soils, plowing and furrowing tends to result in soil sloughing and flowing causing excessive seed burial. Land imprinting (Dixon 1980), which depresses furrows into the soil, may have potential for increasing establishment on these unstable soils (Haferkamp et al.)[3]. The effects of specific mechanical treatments such as pitting or furrowing, and chemical or organic amendments such as gypsum or mulch on seedling establishment varies with the site conditions and seeded species (Malcolm 1972).

Deep plowing may be beneficial to growth by increasing root penetration, infiltration rates and leaching (Smith and Stoneman 1970, Sandoval and Reichman 1971). However, mixing of a sodic horizon with surface soil by plowing can reduce establishment and production of seeded species (Mueller et al. 1985). The fact that plowing of some soils may decrease emergence but increase seedling establishment by reducing weeds (Wood et al. 1982) emphasizes the importance of competition control to successful revegetation of arid areas.

Mulching may improve seedbed water availability by reducing evaporation and salt movement to the surface (Fanning and Carter 1963, Malcolm 1972).

_____

[3] Haferkamp, M.R., B.C. Ganskopp, R.F. Miller and F.A. Sneva. Drilling versus imprinting for establishing crested wheatgrass in the Northern Great Basin (submitted to Journal Range Management).

The cost and quantity of organic or chemical amendments required to improve dryland saline soils may prohibit their use (Mueller et al. 1985). However, spot applications to improve plant establishment may be feasible (Jones 1967).

Cultural seedbed modifications may not be effective enough to ensure successful establishment from direct seeding on some harsh sites (Brown 1962). On many other sites successful revegetation may be possible by using a precise combination of treatments. A good example of this is niche-seeding developed in Australia (Malcolm and Allen 1981). The method involves plowing a small furrow to help collect water and to form a ridge on which to seed and avoid later waterlogging. Shrub seeds are deposited in 1.5 to 2-m intervals in a V-shaped niche or groove created by a press-wheel on the ridge. The niche helps place the seed below the zone of salt accumulation at the peak of the ridge. The seeds are covered with a spot mulch to reduce evaporation and salt accumulation and the surface is sprayed with black latex paint to increase seedbed temperatures and early spring germination (Malcolm et al. 1982, Malcolm and Swaan 1985). This method has been very successful in establishing salt-tolerant shrubs from direct seeding in Western Australia (Kok et al. 1986). Determination of successful site and species-specific tillage and planting methods can be facilitated if measurements are made of temperature, water potential and salinity of treatments as well as biological responses.

Transplanting may be the only way possible to establish plants on some harsh and variable sites (Van Epps and McKell 1980). Transplanting increases establishment by allowing fertilization or mycorrhizal innoculation for vigorous growth, and by permitting planting during favorable seasons and placement of roots below saline surface soils (McKell 1986). Techniques for the culture and propagation of salt tolerant shrubs are being developed as well as transplanting recommendations for the field (Institute for Land Rehabilitation 1979, Van Epps and McKell 1980, Aldon 1984, McArthur et al. 1984, Shaw and Monsen 1984, Stevens and Van Epps 1984). Mass production of plants of a specific genotype is possible by in vitro culture techniques (McKell 1986).

AMELIORATION OF SALINE RANGE SOILS

Traditional reclamation of saline agricultural soils has been by irrigation and drainage to leach the salts and application of gypsum to replace the sodium with calcium on sodic soils. Although it appears now that the amount of water needed for leaching is less than that previously thought, (Bresler et al. 1982), artificial leaching is not economically feasible for most range soils. Initial irrigation to increase seedling establishment may be possible and desirable for some revegetation projects, but seeded species should be drought and salt-tolerant enough to persist without irrigation, once established. Application of gypsum is expensive due to the amount usually needed (Carter et al. 1977) and its reclamation of sodic soils under natural precipitation could be very slow (Sharma 1971).

Nulsen (1986) emphasizes the importance of understanding the hydrological conditions leading to soil salination before determining reclamation procedures. Salination may be the result of irrigation with saline water or a raising of the water table due to vegetation clearing. Nonsodic soils salinized in these cases may be reclaimed by natural leaching once salination is stopped if soil textures allow high infiltration rates. In such cases, salt-tolerant plants could be sown initially and replaced with more desirable, less tolerant, forage species as salinity is reduced (Hamilton and Lang 1978). A high water table which causes a saline seep can be reduced and the seep reclaimed by revegetating the recharge area with forages that have high water use such as alfalfa (Medicago sativa L.) (Halvorson and Reule 1980). Greenwood (1986) recommends and gives guidelines on the use of deep-rooted phreatophytic and halophytic plants to maximize transpiration to lower the water table of saline seep areas. Of course, sub-irrigation from a shallow water table may allow increased production of salt-tolerant plants on some arid rangelands.

Deep plowing and mixing of calcareous and coarse-textured subsoil with sodic surface soil has been successful in reclaiming some saline-sodic soils (Bresler et al. 1983).

The possibility of biological desalination has been suggested by Boyko (1966). The idea is that cropping of salt-accumulating plants can reduce soil salinity (Chaudhri et al. 1964). Green and Snow (1939) found that irrigated Atriplex muelleri Benth. removed 650 kg of sodium per hectare. This amount was minute compared to the sodium in the soil profile. Zahran and Wahid (1982) were able to detect differences in soil salinity before and after cropping salt-accumulating Juncus spp. Biological desalination is probably impractical on rangelands (Malcolm 1986). The amount of salt actually removed from the site by grazing animals would be negligible. The most practical treatment of saline rangelands is in the establishment and proper management of adapted forage species.

LITERATURE CITED

Aldon, E.F. 1984. Methods for establishing fourwing saltbush (Atriplex canescens (Pursh) Nutt.) on disturbed sites in the Southwest. p. 265-268. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of Atriplex and related chenopods. USDA Forest Service and Range Experiment Station. General Tech. Report INT-72. Ogden, Utah.

Asay, K.H. and R.P. Knowles. 1985. Current status and future of introduced wheatgrasses and wildryes for rangeland improvement. p. 109-116. In: Symposium: Range plant improvement. Proceedings selected papers presented at the 38th annual meeting Society for Range Management. Denver, Colorado.

Ashraf, M., T. McNeilly and A.D. Bradshaw. 1986. The potential for evolution of salt (NaCl) tolerance in seven grass species. New Phytologist 103:299-309.

Beadle, N.C.W. 1952. Studies in halophytes. I The germination of the seed and establishment of the seedlings of five species of Atriplex in Australia. Ecology 33:49-62.

Bernstein, L. 1961. Osmotic adjustment of plants to saline media. I. Steady State. Amer. J. of Bot. 48:909-918.

Bernstein, L. 1964. Salt tolerance of plants. Agricultural Information Bulletin No. 283. USDA Government Printing Office, Washington, D.C.

Bettenay, E. 1986. Salt affected soils in Australia. Reclam. and Reveg. Res. 5:167-179.

Bleak, A.T., N.C. Frischknecht, A.D. Plummer and R.E. Eckert, Jr. 1965. Problems in artificial and natural revegetation of the arid shadscale vegetation zones of Utah and Nevada. J. Range Manage. 18:59-65.

Boyko, H. (ed.). 1966. Salinity and aridity: new approaches to old problems. Junk, The Hague.

Breckle, S.W. 1975. Okologie und zu den Mineralstoffverhaltnissen absalzender und nichtabsalzender Xerohalophyten, Habilitationsschrift, Universitat Bonn.

Bresler, E., B.L. McNeal and D.L. Carter. 1982. Saline and sodic soils. Springer-Verlag, New York.

Brown, L.L. 1962. Establishment of forage plants on difficult salt-desert range sites. M.S. Thesis. University of Nevada, Reno.

Caldwell, M.M. 1974. Physiology of desert halophytes. p. 355-379. In: R.J. Reimold and W.H. Queen (eds.), Ecology of halophytes. Academic Press, New York.

Caldwell, M.M. 1985. Cold desert. p. 198-256. In: B.F. Chabot and H.A. Mooney (eds.). Physiological ecology of North American plant communities. Chapman and Hall, New York.

Campbell, R.B., C.A. Bower and L.A. Richards. 1948. Change of electrical conductivity with temperature and the relation of osmotic pressure to electrical conductivity and ion concentrations for soil extracts. Soil Science Soc. of Amer. Proc. 13:66-69.

Carlson, J.R. 1984. Atriplex cultivar development. p. 176-182. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of Atriplex and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

Carter, D.L. 1975. Problems of salinity in agriculture. p. 25-35. In: A. Poljakoff-Mayber and J. Gale (eds.) Plants in saline environments. Spring-Verlag, New York.

Carter, M.R., R.R. Cairns and G.R. Webster. 1977. Amelioration of a brown solodized soil by surface application of gypsum plus ammonium nitrate. Can. J. Soil Sci. 57:139-145.

Chapman, V.J. 1975. The salinity problem in general, its importance, and distribution with special reference to natural halophytes. p. 7-24. In: A. Poljakoff-Mayber and J. Gale (eds.) Plants in saline environments. Springer-Verlag, New York.

Chaudhri, I.I., B.H. Shah, N. Naqui and I.A. Mallick. 1964. Investigations on the role of Suaeda fruticosa Forsk in the reclamation of saline and alkaline soils in West Pakistan plains. Plant and Soil 21:1-7.

Clarke, L.D. and N.E. West. 1969. Germination of Kochia americana in relation to salinity. J. Range Manage. 22:286-287.

Cluff, G.J., R.A. Evans and J.A. Young. 1983. Desert saltgrass seed germination and seedbed ecology. J. Range Manage. 36:419-422.

Cowling, S.W. 1969. A study of vegetation activity patterns in a semiarid environment. Ph.D. Thesis. University of New England, Armidale.

Dewey, D.R. 1960. Salt tolerance of twenty-five strains of Agropyron. Agron. J. 52:631-635.

Dewey, D.R. 1962. Breeding crested wheatgrass for salt tolerance. Crop Sci. 2:403-407.

Dixon, R.M. 1980. Rangeland imprinter. p. 8-10. In: 34th annual report, vegetative rehabilitation and equipment workshop. USDA Forest Service Equipment Development Center, Missoula, Montana.

Dudal, R. and M.F. Purnell. 1986. Land resources: salt-affected soils. Reclam. and Reveg. Res. 5:1-9.

Eckert, R.E., Jr. and F.E. Kinsinger. 1960. Effects of Halogeton glomeratus leachate on chemical and physical characteristics of soils. Ecology 41:785-790.

Eckert, R.E., Jr., A.D. Bruner and G.L. Klomp. 1973. Productivity of tall wheatgrass and Great Basin wildrye under irrigation on a greasewood-rabbitbrush range site. J. Range. Manage. 26:286-288.

Eckert, R.E., Jr., F.F. Peterson, M.S. Meurisse and J.L. Stephens. 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. J. Range Manage. 39:414-420.

Eisenberg, J., J. Dan and H. Koyumdjisky. 1982. Relationships between moisture penetration and salinity in soils of the northern Negev (Israel). Geoderma 28:313-344.

El Hamrouni, A. 1986. Atriplex species and other shrubs in range improvement in North Africa. Reclam. and Reveg. Res. 5:151-158.

Epstein, E. 1972. Mineral nutrition of plants: principles and perspectives. John Wiley, New York.

Evans, R.A., H.R. Holbo, R.E. Eckert, Jr., and J.A. Young. 1970. Functional environment of downy brome communities in relation to weed control and revegetation. Weed Science 18:154-162

Fanning, C.D. and D.L. Carter. 1963. The effectiveness of a cottonburr mulch and a ridge-furrow system in reclaiming saline soils by rainfall. Soil Sci. Soc. Amer. Proc. 27:703-706.

Fisher, M.J. and P.J. Skerman. 1986. Salt tolerant forage plants for summer rainfall areas. Reclam. and Reveg. Res. 5:263-284.

Francois, L.E. and J.R. Goodin. 1972. Interaction of temperature and salinity on sugar beet germination. Agron. J. 64:272-273.

Francois, L.E. and E.V. Maas (eds.). 1978. Plant responses to salinity: an indexed bibliography. USDA Agricultural Research Service, Agricultural Reviews and Manuals, Western Series, No. 6. U.S. Salinity Laboratory, Riverside, California.

Francois, L.E. and E.V. Maas (eds.). 1985. Plant responses to salinity. A supplement to an indexed bibliography. USDA Agricultural Research Service, ARS-24. U.S. Salinity Laboratory, Riverside, California.

Frelich, J.R., E.H. Jensen and R.O. Gifford. 1973. The effect of crust rigidity and osmotic potential on emergence of six grass species. Agron. J. 65:26-29.

Gee, G.W., A. Bauer and R.S. Decker. 1978. Physical analyses of over-burden materials and mine land soils. p. 665-686. In: Reclamation of drastically disturbed lands. American Society of Agronomy, Madison, Wisconsin.

Green, H. and O.W. Snow. 1939. Soil improvement in the Sudan Gezira. Jour. Agric. Sci. 29:1-34.

Greenwood, E.A.N. 1986. Water use by trees and shrubs for lowering saline ground water. Reclam. and Reveg. Res. 5:423-434.

Hadas, A. and D. Russo. 1974a. Water uptake by seeds as affected by water stress, capillary conductivity and seed-soil contact. I. Experimental study. Agron. J. 66:647-652.

Hadas, A. and D. Russo. 1974b. Water uptake by seeds as affected by water stress, capillary conductivity and seed-soil contact. II. Analysis of experimental data. Agron. J. 66:647-652.

Halvorson, A.D. and C.A. Reule. 1980. Alfalfa for hydrologic control of saline seeps. Soil Sci. Soc. Amer. J. 44:370-374.

Hamilton, G.J. and R.D. Lang. 1978. Reclamation and control of dryland salt affected soils. J. Soil Cons. Ser., New South Wales 34:28-36.

Hansen, D.J., P. Dayanandan, P.B. Kaufman and J.D. Brotherson. 1976. Ecological adaptations of salt marsh grass, Distichlis spicata (Gramineae), and environmental factors affecting its growth and distribution. Amer. J. Bot. 63:635-650.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hayward, H.E. and C.H. Wadleigh. 1949. Plant growth on saline and alkali soils. p. 1-38. In: A.G. Norman (ed.). Advances in Agronomy Vol. I. Academic Press, New York.

Hegarty, T.W. 1978. The physiology of seed hydration and dehydration, and the relation between water stress and the control of germination: a review. Plant, Cell and Environment 1:101-119.

Heydecker, W. and P. Coolbear. 1977. Seed treatments for improved performance -- survey and attempted prognosis. Seed Sci. and Tech. 5:353-425.

Hoffman, G.J. and M.C. Shannon. 1986. Relating plant performance and soil salinity. Reclam. and Reveg. Res. 5:211-225.

Hsaio, T.E., E. Acevedo, E. Fereres and D.W. Henderson. 1976. Stress metabolism. Philosophical Transactions Royal Society London Bulletin. 273:479-500.

Hyder, S.Z. and S. Yasmin. 1972. Salt tolerance and cation interaction in alkali sacaton at germination. J. Range Manage. 25:390-392.

Institute for Land Rehabilitation. 1979. Selection, propagation and field establishment of native plant species on disturbed lands. Bulletin 500. Utah Agricultural Experiment Station, Logan, Utah.

Jackson, E.A., G. Blackburn, and A.R.D. Clarke. 1956. Seasonal changes in soil salinity at Tintinara, South Australia. Aust. J. of Agric. Res. 7:20-44.

Jefferies, R.L. and M.G. Pitman. 1986. Perspectives of the biology of halophytes in natural habitats in relation to forage production. Reclam. and Reveg. Res. 5:227-243.

Jensen, C.R. 1982. Effect of soil water osmotic potential on growth and water relationships in barley during soil water depletion. Irrig. Sci. 3:111-121.

Jones, R.M. 1967. Investigations of seedling establishment in a reclaimed scald. Jour. Soil Cons. New South Wales 23:187-191.

Jones, R. (ed.). 1970. The biology of Atriplex. Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia.

Kernick, M.D. 1986. Forage plants for salt affected areas in developing countries. Reclam. and Reveg. Res. 5:451-459.

Khan, A.A., N.H. Peck and C. Samimy. 1980-81. Seed osmoconditioning: physiological and biochemical changes. Israel J. Bot. 29:133-144.

Khan, M.A. and I.A. Ungar. 1984. The effect of salinity and temperature on the germination of polymorphic seeds and growth of Atriplex triangularis. Wild. Amer. J. B. 71:481-489.

Kok, B., P.R. George and J. Stretch. 1986. Saltland revegetation with salt-tolerant shrubs. Reclam. and Reveg. Res. 5:501-507.

Koller, D. and A. Hadas. 1982. Water relations in the germination of seeds. p. 402-431. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler (eds.). Physiological plant ecology II. Water relations and carbon assimilation. Encyclopedia of Plant Physiology. New Series, Vol. 12B. Springer-Verlag, New York.

Lehouerou, H.N. 1986. Salt-tolerant plants of economic value in the Mediterranean Basin. Reclam. and Reveg. Res. 5:319-341.

Leigh, J.H. 1986. Forage value and utilization of chenopod dominated shrubland. Reclam. and Res. 5:387-402.

Levitt, J. and P.C. Hamm. 1943. A method for increasing the rate of seed germination of Taraxacum kok-saghyz. Plant Phys. 18:288-293.

Levitt, J. 1980. Responses of plants to environmental stress. Vol. II. Water, radiation, salts and other stresses. Academic Press, New York.

Maas, E.V. 1986. Salt tolerance of plants. Applied Agric. Res. 1:12-26.

Maas, E.V. and G.J. Hoffman. 1977. Crop salt tolerance-current assessment. J. Irr. and Drain. Div., Amer. Soc. Civil Eng. 103:115-134.

Macke, A. and I.A. Ungar. 1971. The effect of salinity on seed germination and early growth of Puccinellia nuttalliana. Can. J. Bot. 49:515-520.

Magistad, O.C. 1945. Plant growth relations on saline and alkali soils. Bot. Review II:181-230.

Malcolm, C.V. 1972. Establishing shrubs in saline environments. Department of Agriculture, Western Australia. Tech. Bull. 14.

Malcolm, C.V. 1986. Production from salt affected soil. Reclam. and Reveg. Res. 5:343-361.

Malcolm, C.V. and R.J. Allen. 1981. The Mallen niche seeder for plant establishment on difficult sites. Aust. Range. J. 3:106-109.

Malcolm, C.V., B.J. Hillman, T.C. Swaan, C. Denby, D. Carlson and M. D'Antuno. 1982. Black paint, soil amendment and mulch effects on chenopod establishment in a saline soil. J. Arid Envir. 5:179-189.

Malcolm, C.V. and T.C. Swaan. 1985. Soil mulches and sprayed coatings and seed washing to aid chenopod establishment on saline soil. Aust. Range. J. 7:22-28.

Manohar, M.S., S.B. Bhan and R. Prasad. 1968. Germination in lower osmotic potentials as an index of drought tolerance in crop plants. A review. Annals Arid Zone 7:82-92.

McArthur, E.D., A.C. Blauer and G.L. Noller. 1984. Propagation of fourwing saltbush (Atriplex canescens (Pursh) Nutt.) by stem cuttings. p. 261-264. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of Atriplex and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

McGinnies, W.J. 1959. The relationship of furrow depth to moisture content of soil and to seedling establishment on a range soil. Agron. J. 51:13-14.

McGinnies, W.J. 1960. Effects of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-163.

McKell, C.M. 1986. Propagation and establishment of plants on arid saline land. Reclam. and Reveg. Res. 5:363-375.

McKell, C.M., J.R. Goodin and R.L. Jefferies. 1986. Saline land of the United States of America and Canada. Reclam. and Reveg. Res. 5:159-165.

Midgley, S.J., J.W. Turnbull and V.J. Hartney. 1986. Fuel-wood species for salt-affected soils. Reclam. and Reveg. 5:285-303.

Miller, D.E. and R.O. Gifford. 1974. Modifications of soil crusts for plant growth. p. 7-16. In: J.W. Cary and D.D. Evans (eds.). Soil crusts. Agricultural Experiment Station Technical Bulletin 214. University of Arizona, Tucson.

Mozafar, C.A. and J.R. Goodin. 1970. Vesiculated hairs: A mechanism for salt tolerance in _Atriplex halimus_ L. Plant Phys. 45:62-65.

Mueller, D.M., R.A. Bowman, W.J. McGinnies. 1985. Effects of tillage and manure on emergence and establishment of Russian wildrye in a saltgrass meadow. J. Range Manage. 38:497-500.

Niehman, R.H. and E.V. Maas. 1978. The energy charge of salt-stressed plants. p. 121. Abstracts of Sixth International Biophysics Congress, September 3-9, Kyoto, Japan.

Nord, E.C. and G.R. Van Alta. 1960. Saponon-a seed germination inhibitor. Forest Sci. 6:350-353.

Norton, B.E. 1986. Guidelines for determining stocking rates for saline shrubland. Reclam. and Reveg. Res. 5:402-422.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecol. and Syst. 4:25-51.

Nulsen, R.A. 1986. Management to improve production from salt affected soils. Reclam. and Reveg. Res. 5:197-209.

Odegbaro, O.A. and O.E. Smith. 1969. Effects of kinetin, salt concentration and temperature on germination and early seedling growth of _Lactuca sativa_ L. J. Amer. Soc. Hort. Sci. 94:167-170.

Osmond, C.B., O. Bjorkman and D.J. Anderson. 1980. Physiological processes in plant ecology. Toward a synthesis with _Atriplex_. Springer-Verlag, New York.

Papke, K.G. 1976. Evaporites and brines in Nevada playas. Nevada Bureau of Mines and Geology, Bulletin 87. University of Nevada, Reno.

Plummer, A.P. 1966. Experience in improving salt desert shrub range by artificial planting. p. 130-146. In: Salt desert shrub symposium. Department of Interior, Bureau of Land Management. Cedar City, Utah.

Poljakoff-Mayber, A. and J. Gale (eds.). 1975. Plants in saline environments. Springer-Verlag, New York.

Potter, R.L., D.N. Ueckert, J.L. Petersen and M.L. McFarland. 1986. Germination of fourwing saltbush seeds: interaction of temperature, osmotic potential and pH. J. Range Manage. 39:43-46.

Rajpurohit, K.S. and D.N. Sen. 1980. Osmotic potentials of plants and soils of Pachpadra salt basin in Thar desert. In: Proc. international symposium on arid zone research and development. Jodhpur, India: Central Arid Zone Research Institute.

Ratner, E.I. 1935. The influence of exchangeable sodium in the soil on its properties as a medium for plant growth. Soil Sci. 40:459-468.

Rauser, W.E. and W.L. Crowle. 1963. Salt tolerance of Russian wildrye grass in relation to tall wheatgrass and slender wheatgrass. Can. J. of Plant Sci. 43:397-407.

Redmann, R.E. 1974. Osmotic and specific ion effects on the germination of alfalfa. Can. J. Bot. 52:803-808.

Rickard, W.H 1965. Sodium and potassium accumulation by greasewood and hopsage leaves. Bot. Gazette 126:116-119.

Roundy, B.A. 1983. Response of basin wildrye and tall wheatgrass to salination. Agron. J. 75:67-71.

Roundy, B.A. 1984. Estimation of water potential components of saline soils of Great Basin rangelands. Soil Sci. Soc. of Amer. J. 48:645-650.

Roundy, B.A. 1985a. Emergence and establishment of basin wildrye and tall wheatgrass in relation to moisture and salinity. J. Range Manage. 38:126-131.

Roundy, B.A. 1985b. Germination and seedling growth of tall wheatgrass and basin wildrye in relation to boron. J. Range Manage. 38:266-270.

Roundy, B.A. 1985c. Root penetration and shoot elongation of tall wheatgrass and basin wildrye in relation to salinity. Can. J. Plant Sci. 65:335-343.

Roundy, B.A., J.A. Young and R.A. Evans. 1984. Surface soil and seedbed ecology in salt desert plant communities. p. 66-74. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of _Atriplex_ and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

Roundy, B.A. and J.A. Young. 1985. Salt deserts of the Great Basin. p. 39-49. In: Symposium: Cultural, physical, and biological characteristics of the range livestock industry in the Great Basin. Proc. selected papers presented at the 38th Annual Meeting of the Society for Range Management. Denver, Colorado.

Roundy, B.A., J.A. Young and R.A. Evans. 1985. Germination of basin wildrye and tall wheatgrass in relation to osmotic and matric potential. Agron. J. 77:129-135.

Runciman, H.V. 1986. Forage production from salt affected wasteland in Australia. Reclam. and Reveg. Res. 5:17-29.

Ryan, J., S. Miyamoto and J.L. Stroehlein. 1975. Salt and specific ion effects on germination of four grasses. J. Range Manage. 28:61-64.

Sandoval, F.M. and W.L. Gould. 1978. Improvement of saline - and sodium - affected disturbed lands. p. 485-504. In: Reclamation of drastically disturbed lands. Amer. Soc. of Agron., Madison, Wisconsin.

Sandoval, F.M. and G.A. Reichman. 1971. Some properties of solonetzic (sodic) soil in western North Dakota. Can. J. Soil Sci. 51:143-155.

Schmehl, W.R. and B.D. McCaslin. 1973. Some properties of spent oil shale significant to plant growth. p. 7-25. In: M.B. Bloch and P.D. Kilburn (eds.). Processed oil shale revegetation studies, 1965-1973. Atlantic Richfield Co., Colony Development Operation.

Shannon, M.C. 1980. Genetics of salt tolerance: New challenges. p. 271-282. In : A. San Pietro (ed.). Biosaline research. Plenum Press, New York.

Sharma, M.L. 1971. Physical and physio-chemical changes in the profile of a sodic soil treated with gypsum. Aust. J. Soil Res. 9:73-82.

Sharma, M.L. 1973. Simulation of drought and its effect on germination of five pasture species. Agron. J. 65:982-987.

Sharma, M.L. 1976. Interaction of water potential and temperature on germination of three semiarid plant species. Agron. J. 68:390-394.

Shaw, N. and S.B. Monsen. 1984. Nursery propagation and out planting of bareroot chenopod seedlings. p. 251-260. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of Atriplex and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

Simanton, J.R. and G.L. Jordan. 1986. Early root and shoot elongation of selected warm-season perennial grasses. J. Range Manage. 39:63-67.

Smith, S.T. and T.C. Stoneman. 1970. Salt movement in bare saline soils. Western Australia Department Agriculture Technical Bulletin 4.

Springfield, H.W. 1966. Germination of four-wing saltbush seeds at different levels of moisture stress. Agron. J. 58:159-160.

Stevens, R. and G.A. Van Epps. 1984. Seeding techniques to improve establishment of forage kochia (Kochia prostrata (L.) Schrad.) and four-wing saltbush (Atriplex canescens (Pursh) Nutt.). p. 269-272. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of Atriplex and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

Strogonov, B.P. 1962. Physiological basis of salt tolerance of plants. (Translated edition). Israel Program for Scientific Translation, Jerusalem.

Stutz, H.C. and J.R. Carlson. 1985. Genetic improvement of saltbush (Atriplex) and other chenopods. p. 197-200. In: Symposium: Range plant improvement. Proc. selected papers presented at the 38th Annual Meeting of the Society for Range Management. Denver, Colorado.

Teakle, L.J.H. and G.H. Burville. 1938. Movement of soluble salts in soils under light rainfall conditions. J. of the Dept. of Agric. of West. Aust. 15:218-245.

Thomson, W.W. 1975. The structure and function of salt glands. p. 118-146. In: A. Poljakoff-Mayber and J. Gale (eds.). Plants in saline environments. Springer-Verlag, New York.

Tiedemann, A.R., E.D. McArthur, H.C. Stutz, R. Stevens and K. Johnson (compilers). 1984. Proc. -- symposium on the biology of Atriplex and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

Turner, N.C. and M.M. Jones. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. p. 87-103. In: N.C. Turner and P.J. Kramer (eds.). Adaptation of plants to water and high temperature stress. John Wiley, New York.

Twitchell, L.T. 1955. Germination of four-wing saltbush seed as affected by soaking and chloride removal. J. Range Manage. 8:218-220.

Ungar, I.A. 1974. Inland halophytes of the United States. p. 235-305. In: R.J. Reinnold and W.H. Queen (eds.). Ecology of halophytes. Academic Press, New York.

Ungar, I.A. 1978. Halophyte seed germination. Bot. Review 44:232-264.

Ungar, I.A. and F. Capilupo. 1969. An ecological life history study of _Suaeda depressa_ (Pursh) Wats. Advances in Frontiers in Plant Science 23:137-158.

Ungar, I.A. and W. Hogan. 1970. Seed germination in _Iva annua_ L. Ecology 51:150-154.

U.S. Salinity Laboratory Staff. 1954. Diagnosis and improvement of saline and alkali soils. Agriculture Handbook No. 60. USDA Government Printing Office, Washington D.C.

Van Epps, G.A. and C.M. McKell. 1980. Revegetation of disturbed sites in the salt desert range of the Intermountain west. Land Rehabilitation Series No. 5. Utah Agricultural Experiment Station, Logan, Utah.

Ward, J.M. 1967. Studies in ecology of a shell barrier beach. III. Vegetatio 15:77-112.

Williams, D.G. 1972. Ecological studies on the shrub-steppe of the western Riverina, New South Wales, Ph.D. thesis. Australian National University, Canberra.

Wood, J.G. 1925. The selective absorption of chlorine ions and absorption of water by the leaves of the genus _Atriplex_. Aust. J. Exp. Biol. and Med. Sci. 2:45-56.

Wood, M.K., R.E. Eckert, Jr., W.H. Blackburn and F.F. Peterson. 1982. Influence of crusting soil surfaces on emergence and establishment of crested wheatgrass, squirreltail, thurber needlegrass and fourwing saltbush. J. Range Manage. 35:282-287.

Young, J.A. and R.A. Evans. 1981. Germination of Great Basin wildrye seeds collected from native stands. Agron. J. 73:917-920.

Young, J.A., R.A. Evans, B. Roundy and G. Cluff. 1983. Moisture stress and seed germination. USDA Agricultural Research Service ARM-W-36. Oakland, California.

Young, J.A., R.A. Evans, B.A. Roundy and G.J. Cluff. Ecology of seed germination in representative Chenopodiaceae. p. 159-165. In: A.R. Tiedemann et al. (compilers). Proc. -- symposium on the biology of _Atriplex_ and related chenopods. USDA Forest Service Intermountain Forest and Range Experiment Station. General Technical Report INT-72. Ogden, Utah.

Young, J.A. and R.A. Evans. 1986. Erosion and deposition of fine sediments from playas. J. of Arid Environ. 10:103-115.

Young, J.A., R.A. Evans, B.A. Roundy and J.A. Brown. 1986. Dynamic landforms and plant communities in a pluvial lake basin. Great Basin Naturalist 46:1-21.

Zahran, M.A. and A.A. Abdel Wahid. 1982. Halophytes and human welfare. In: D.N. Sen and K.S. Rajpurohit (eds.). Task for vegetation science Vol. 2. Junk, The Hague.

Zaller, S. and A. Mitchell. 1970. Pasture species for nonirrigation of salt-affected cond. In: Proc. 11th International Grass Congress.

INFRASPECIFIC VARIATION IN GERMINATION PATTERNS OF
RANGELAND SHRUBS AND ITS RELATIONSHIP TO SEEDING
SUCCESS

S. E. Meyer[1], E. D. McArthur[2], and S. B. Monsen[3]

ABSTRACT

Infraspecific variation in rangeland shrub seed
germination has been studied in few species.
Available data suggest that ecologically
meaningful patterns exist, but more detailed
investigations are needed to develop useful
predictive models. Within-species differences in
germination patterns could have a major effect on
the outcome of artificial seedings on particular
site types.

INTRODUCTION

Shrub species are important components of range
and wildlife habitats in the semiarid western
United States. Some habitats have become degraded
through inappropriate management practices over
the last century or more. The need for artificial
seeding programs which include shrub species has
been recognized since the 1930's, and efforts to
develop suitable plant material and effective
seeding methods for shrub-grass-forb mixtures have
been intensive (Plummer et al. 1968). Work on
shrub selection and evaluation has culminated in
the release of several shrub cultivars and has
provided a wealth of knowledge on ecotypic
differentiation (McArthur et al. 1979; Davis 1983;
Monsen and Davis 1985). Seed germination and
seedling establishment characteristics of several
range shrubs have been characterized as part of
this effort. But most seed germination studies
have addressed patterns at the species or
subspecies level.

Differences in the germination patterns of
different sources of seed within a species could
explain why some seedings are successful while
others fail under apparently similar
circumstances. At present, these source
differences are largely an unknown quantity, a
source of almost random error. But if the causes
and consequences of within-species germination
variation could be understood and predicted, a
valuable tool for increasing the probability of
acceptable stand establishment would be in our
hands.

[1]Research Associate, Utah Division of Wildlife
Resources, USFS-INT Shrub Sciences Laboratory,
Provo, UT 84601.

[2]Supervisory Research Geneticist, USFS-INT Shrub
Sciences Laboratory, Provo, UT 84601.

[3]Principal Botanist, USFS-INT Shrub Sciences
Laboratory, Provo, UT 84601.

SOURCES OF INFRASPECIFIC VARIATION

The basic function of a germination pattern is
to time germination so that it occurs under
conditions of minimum risk to the resultant
seedling (Koller 1972; Fenner 1985). It often
includes insurance against germination under
conditions which may be immediately favorable
but which are coupled to high risk for the
seedling. Such seed dormancy usually has high
adaptive value in natural stands, but may be a
hindrance to artificial stand establishment
(Monsen and McArthur 1985).

If seed germination patterns can be explained
in terms of their adaptive significance, they
must ultimately be under genetic control. The
genetic control of seed dormancy has been
studied systematically in only a few species
(Morley 1958; Harper and McNaughton 1960;
Witcomb and Whittington 1972). Indications are
that, while the limits of variation are set
genetically and are heritable, the influence of
environmental factors during seed development on
the mother plant is profound and far-reaching
(Gutterman 1980; Cresswell and Grime 1981;
Silvertown 1984). Thus, the simple solution of
artificially selecting plants with desirable
seed germination or even seed quality traits is
greatly complicated.

Within-species variation in germination
characteristics can be approached at several
levels. Differences among populations, among
plants in a population, among seeds on an
individual plant, and among harvest dates or
years of production may all contain useful
information. More experimental approaches might
include evaluation of differences in genetically
similar materials ripened under contrasting
conditions or genetically contrasting materials
ripened under similar conditions. The common
gardens and outplantings used for evaluation of
plant materials at the post-establishment stage
could provide the necessary contrasts.

Many important western shrubs are wide-ranging
and occur in a variety of habitats. If
between-population differences in germination
response are adaptive, we would expect a
correlation between response to a particular
laboratory condition and habitat characteristics
at the site of seed origin. The readiness to
germinate under a given condition should be
inversely related to the risk to seedlings
produced under that condition in the field.
Thus a 2C temperature regime is a signal for
germination at the time of lowest risk in a
rubber rabbitbrush ecotype from a low desert
environment, while it signals extreme frost risk
to a montane ecotype (McArthur et al. 1987).
This result might at first appear counter-
intuitive. Warm climate sources germinate
faster in the cold than cold-climate sources.

A similarly counter-intuitive result was
obtained by Young and Evans (1981a) in their
work with the perennial grass basin wildrye
(Elymus cinereus Scribn. and Merr.). Sources
collected from highly saline soils had poorer

germination at high osmotic potentials than sources from less saline soils. In other words, the saline soil sources were protected from germinating at osmotic potentials which were likely to exceed seedling tolerance as drying proceeded. The sources from less alkaline soils largely lacked this protection, since in their environment the salinity was not so likely to exceed seedling tolerance. It was the ability to prevent germination at hazardous salinities that characterized the saline soil collections.

Demonstration of a relationship between seed germination patterns and collection site characteristics is only the first step in understanding the nature of the variation. Many workers have concluded that such differences are ecotypic (genetic) without any experimental basis (Stearns and Olsen 1958; Barnes 1967). It is just as plausible that a species could evolve a generalist seed germination genotype which interacts with the environment to produce a germination response appropriate to that habitat.

Since environmental factors during seed maturation are important in determination of seed germination characteristics as well as seed quality, seed produced at a given site in a given year may not behave according to a particular model even if the model is generally valid. The interaction between genotype and environment is not necessarily precise, especially for long-lived plants which can afford years of low seed production or the production of imperfectly adapted seeds. Moreover, what constitutes 'perfectly-adapted seed' can vary from year to year or even from season to season depending on weather patterns, disturbance events, and other factors. In the long run, retention of the ability to produce seeds which vary in their requirements may be selected for.

RANGE SHRUB CASE HISTORIES

The literature on seed germination of western North American shrubs is voluminous, but studies on infraspecific variation are quite scarce. Much of the research was ancillary to more immediately pressing problems of production and harvest, quality evaluation, and field sowing techniques. In this review we will focus on five key species, reexamining published accounts and adding some information recently generated in our laboratory. These are among the few native species for which sufficient information is available to permit even tentative conclusions about infraspecific variation.

Winterfat (Ceratoides lanata [Pursh] Howell)

Winterfat is widely acclaimed as an excellent drought-tolerant winter forage plant for both big game and livestock (Stevens et al. 1977). Seeds ripen in the fall and are generally acknowledged to be short-lived both in the field and in dry storage (Springfield 1968a). Early studies by Hilton (1941) and Reidl et al. (1964) established the basic germination syndrome. Seeds may be

dormant when shed but afterripen quickly in dry storage (within three months), after which they germinate within fourteen days over a wide range of temperatures from 10C to 25C (Springfield 1972b). Dettori et al. (1984) confirmed this result.

The seed is also relatively quick to germinate at near-freezing temperatures (Jorgensen unpublished data on file at Ephraim, Utah). The afterripening requirement in fresh seed can sometimes be circumvented by a short prechill period (Allen et al. 1987). Hilton (1941) reported that holding the seed at freezing temperatures for one month completely broke dormancy of one fresh lot, while temperatures which alternated between -4C and 15C produced full germination in this same lot in seven days.

Springfield reported on within-population differences in winterfat seed germination (Springfield 1968a, 1972a, 1972b). Working with seeds collected in four different years from the same group of plants at Corona, NM, he found major year-to-year differences in both viability loss through time and rate of afterripening. There were no major year-to-year differences in the temperature response of afterripened seeds. Ten-day germination percentages in the cold (0C to 7C) were more variable than percentages at higher temperatures, suggesting that year-to-year differences in germination rate in the cold might exist.

Hilton (1941) reported a difference in dormancy/afterripening requirement due to date of harvest within a single year; seed harvested early was much more dormant than late-harvested seed. In an experiment with Corona seed graded into three size classes, Springfield (1973) found that larger seeds had higher and more rapid germination especially at low temperatures. Whether this difference was a consequence of a difference in seed viability or degree of dormancy was not clear.

Springfield (1968b) reported on between-population differences in germination response to temperature and osmotic stress. When subjected to moderate moisture stress, seeds collected at Horse Springs, NM, germinated better at high temperatures than seeds from Corona, while the Corona seeds germinated better at cooler temperatures. Workman and West (1967) also found differences among four Utah sources in the germination response to osmotic stress. They concluded that these differences were ecotypic. No correlation with site characteristics was discussed. A paper dealing with responses of populations from three closely adjacent sites in Utah to different concentrations of various salts came to a similar conclusion (Clark and West 1971).

Moyer and Lang (1975) found that a relatively high-elevation collection had a higher optimum temperature for germination and was slower to germinate in the cold than two lower elevation collections. Dettori et al. (1984) included several sources in their temperature response surface analysis, but none were from known

native stands, and the discussion centers on between-source and between-species differences in seed quality.

The winterfat germination pattern appears to be predictive, i.e., it functions to time germination appropriately sometime during the first year following production, with little carry-over of seed from year to year. Since winterfat occurs over a wide range of sites, differences in timing at different sites would seem to be adaptive, but such differences have only been hinted at by previous researchers.

Fourwing Saltbush (Atriplex canescens [Pursh] Nutt.)

Fourwing saltbush is among the most palatable and useful shrubs on semiarid western ranges (Plummer et al. 1966). Its potential usefulness in revegetation was recognized early (Wilson 1928). A principal problem with fourwing saltbush seed is low fruit fill (Springfield 1970). The unfilled fruits cannot readily be detected or cleaned from the sample, making interpretation of germination percentages difficult. The problem lies in distinguishing between lot-to-lot differences in seed viability/fill versus lot-to-lot differences in the behavior of viable seed. It may seem obvious that differences in germination percentages may be due to one or both of these factors, yet they are rarely separated, especially in the older literature. Springfield recognized this problem, yet did not choose to express his germination results on the basis of filled seeds only.

In contrast to winterfat seeds, fourwing saltbush seeds are apparently long-lived and retain their viability without special storage treatments (Springfield 1968c). They are also reported to have low palatability to rodents and to persist in the seedbank in the field for several years (Everett et al. 1978; Crofts 1977). The seed is mostly dormant when it reaches maturity and requires a more or less lengthy afterripening period (10 months or more). Two sources in dry storage continued to show increases in germinability over a four year period (Springfield 1968c). Fourwing saltbush fruits are commonly dewinged for ease in drilling; dewinging speeds germination somewhat but does not affect the final percentages significantly (Springfield 1970).

Various workers have tried to circumvent the afterripening requirement, with mixed success. Twitchell (1955) reported that leaching chlorides from the fruit wall using a soaking treatment increased germination in a Roswell, NM source, but efforts to reproduce this effect with other sources were unsuccessful (Springfield 1970). Nord and Whitacre (1957) reported that heavy scarification improved germination in two Sonoran Desert lots, but other workers have reported that mechanical scarification damaged seed and reduced germination (Springfield 1970). Efforts to break dormancy using cold stratification were only rarely effective, and dormancy-breaking chemicals such as thiourea and hydrogen peroxide were not helpful. These generally poor and often conflicting results

suggest two things. First, fourwing saltbush seed probably has multiple dormancy mechanisms, and the relative importance of these mechanisms varies from lot to lot. Second, a sizeable fraction of the dormancy in fourwing saltbush appears to be innate rather than predictive in that it does not respond to specific cues but must be gradually lowered through time.

Some work on within-population variation in fourwing saltbush germination patterns has been reported. Gerard (1978) found major differences among plants within a population for 10 populations on the Jornada Plains in New Mexico. Both fruit fill percentages and germination percentages for filled fruits showed the intrapopulation variation. At least some of the difference in germination of filled fruits is probably due to dormancy differences. Gamrath (1972) found differences in fill, germinability, and utricle size among inflorescences on the same plant, but Crofts (1977) failed to confirm these findings.

Factors influencing fruit fill have been examined in some detail. Crofts (1977) concluded that environmental factors influence fill more than genetic factors. Johnson (1975) was only partially able to control fill by manipulating environmental factors. Several of these workers reported that utricle size and percent fill are often inversely correlated.

Fourwing saltbush seed may persist on the plant for several months after reaching maturity. Springfield (1970) reported a difference in germinability due to date of harvest for two sources in two collection years. Nineteen sixty-five Isleta seed showed high germinability whether harvested in fall or spring, while Silverhill seed increased in germinability over this period. Nineteen sixty-six seed of both sources showed a major decrease in germinability for spring-collected seeds. These seeds eventually afterripened in storage and achieved germination percents as high as those of fall-collected seed. Springfield also reported cyclic changes in dormancy through time in dry storage for one Isleta collection. These results suggest complex dormancy mechanisms which are not understood.

Springfield worked extensively on between-population differences in germination pattern in fourwing saltbush. He used seed from eight sites in New Mexico and Arizona, and looked at numerous factors, including effects of storage temperature, germination temperature, and osmotic stress (Springfield 1964, 1966, 1969, 1970). He found major source differences in degree of dormancy, temperature response, and moisture stress response of one-year-old seed, but did not correlate any of these differences with site characteristics, perhaps because the emerging patterns tended to seem counter-intuitive as mentioned above. Table 1 shows Springfield's 1964 data on temperature response in eight sources from New Mexico and Arizona, expressed on the basis of percentage of tetrazolium-viable seed. The 10-month-old

seed was almost completely afterripened, and most viable seed germinated at the intermediate temperature (14C). Lower elevation sources showed more strongly depressed germination at the high temperature (r=+.732, p < .05 for collection site elevation and percentage of tz-viable seeds germinating at 24C). Lower elevation sources also tended to show depressed germination at suboptimal temperatures, though this relationship is only marginally significant statistically (r=+.637, p < .10). Based on these admittedly incomplete data, it appears that sources from harsher, drier sites may have narrower temperature ranges for germination than sources from higher, more mesic sites.

Table 1. Relative germination percentages for eight fourwing saltbush sources from Arizona and New Mexico germinated at three temperatures. Data from Springfield (1964). Percentages are based on estimated viability percentages from tetrazolium staining for the same lots (Springfield 1970).

Source	Elevation (ft.)	Temperature		
		24C	14C	6C
Mountainair	6700	75	100	88
Monica	6600	58	91	91
Flagstaff	6500	55	100	100
Corona	6300	38	77	96
Chevelon	6200	54	62	67
Isleta	5000	63	100	90
Glenwood	4500	14	100	60
Beaver Creek	3500	21	100	60

In Springfield's work with germination response of six of the same sources to osmotic stress, Mountainair seed had the most germination at higher stress levels, even though it was from the highest elevation and possibly the most mesic site (Springfield 1966). He speculated that it might be genetically superior for germination at marginal soil moisture levels. It seems more probable that ability to overcome dormancy under intermediate moisture stress would be more characteristic of seeds from sites with soils which dry slowly. Seeds from more arid sites would be protected by a dormancy mechanism under these conditions.

It should be emphasized that there are seed collections in Springfield's data set which emphatically do not follow these trends. But the tantalizingly incomplete patterns suggest that work with a larger number of sources from diverse sites could be very fruitful. Stutz et al. (1975) mention that polyploid collections of fourwing saltbush tend to have more seed dormancy than diploid collections. This could be related to the fact that polyploid races often occupy

harsher, drier sites that their diploid conspecifics.

Gerard (1978) worked with 10 sources from the Jornada Plains in New Mexico. There were significant between-site differences in both fruit fill and germinability of filled seeds, even though within-site (between-plant) variability was also high. He was unable to correlate these differences with differences in rainfall received during the season of maturation, but did not try correlations with other site environmental parameters.

Antelope Bitterbrush (Purshia tridentata [Pursh] DC.)

Antelope bitterbrush is possibly the most-studied of the western range shrubs, largely because of its high palatability to big game (Basile 1967; Giunta et al. 1978). It was soon realized that bitterbrush seed is essentially completely dormant at harvest (Hormay 1943). Some means of breaking this dormancy, either by manipulating planting time or by treating the seed before sowing, was necessary before acceptable stands could be achieved through artificial seeding. Germination research on bitterbrush has centered on this problem.

Cold stratification during the winter months is the natural mechanism for dormancy-breaking in bitterbrush, and artificial stratification treatments have given consistently good results, although the details of temperature and duration are still under some debate (McConnell 1960; McHenry and Jensen 1967; Young and Evans 1976, 1981b; Meyer et al. 1986). Efforts to circumvent the stratification requirement with dormancy-breaking chemicals have also been quite successful. Treatments have included GA3 (McConnell 1960), thiourea (Pearson 1957; Harper 1970; Neal and Sanderson 1976), and hydrogen peroxide (Everett and Meeuwig 1978; Young and Evans 1981b). Nord (1956) refined the embryo excision methods of Hormay (1943); both authors reported that excised embryos germinated readily and normally. Evans and Young (1977) reported that adequately stratified bitterbrush seed was relatively insensitive to germination temperature, but that unstratified seed required alternating temperatures which included a temperature in the stratification range (0C-5C) in order to germinate. Thiourea-treated seed had even wider temperature tolerances (Young and Evans 1981b).

Published studies on within-species variation in bitterbrush germination patterns are almost completely lacking, possibly because the complete dormancy of fresh seed suggests that differences are not of much practical significance. Young and Evans (1976) do report source differences in response to stratification at some periods and temperatures, but they do not present the data by source. Work on hydrogen peroxide soaking suggests source differences in response, especially at treatment

levels which are inadequate to break dormancy completely (Everett and Meeuwig 1978; Young and Evans 1981b). Similar results were obtained by Alderfer (1976) in response to thiourea. Untreated seeds did not germinate, and adequately treated seeds of all sources germinated completely. Source differences were apparent only at intermediate thiourea levels which partially broke dormancy. Alderfer was unable to correlate these differences with site environmental factors. In a recent 20-source experiment in our laboratory, we tested a factorial combination of prechill and water pre-soaking treatments. Source differences were again most apparent in treatments which only partially broke dormancy (fig. 1). Patterns of dormancy in this experiment showed no obvious correlation with collection site characteristics, possibly because most of the seedlots used were four years old and may have undergone changes in storage.

Antelope bitterbrush seeds are long-lived in dry storage (Stevens et al. 1981), but because of their high palatability to rodents they probably only rarely enjoy long life in the field (Everett et al. 1978; Evans et al. 1983). Thus the responses of old seed may not have much ecological relevance under natural conditions. Old seed may be sown artificially, however. It might therefore be useful to know whether the seed changes in a predictable way in dry storage.

Preliminary data from our laboratory suggest that 4-year-old seed is more germinable than freshly-collected seed under conditions of inadequate stratification (Table 2). This information

Table 2. Relative germination percentages (expressed as percentage of tetrazolium-viable seed) for 4-year-old (1982) seed and 2-month-old (1986) seed of antelope bitterbrush subjected to two weeks of cold stratification at 2C followed by a 2-week germination test at 15C.

Source	1982 Seed	1986 Seed
Ada Co., ID	71	6
Middleton, ID	23	12
Gooding, ID	49	0
Celilo, OR	36	6
Janesville, CA	37	10
Wells, NV	43	12
Mtn. Dell, UT	36	7
Ftn. Green, UT	21	5
Mean	40	7
S.E.	5.6	1.4

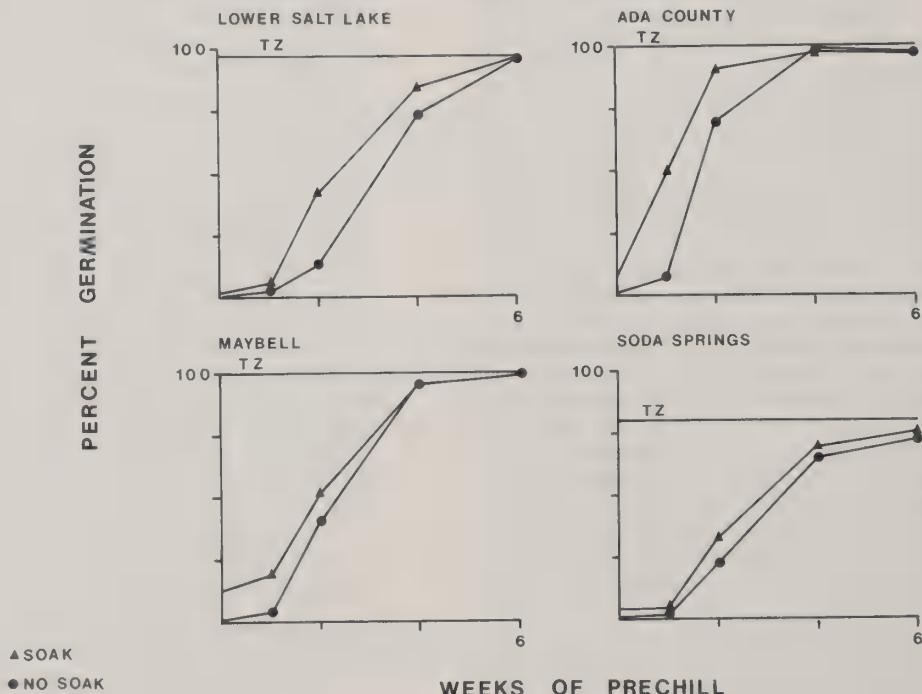Figure 1. Absolute germination percentages of four 1982 (4-year-old) collections of antelope bitterbrush in response to a factorial combination of soaking and prechill treatments. The soak treatment consisted of 24 hours in water at 20C prior to the initiation of prechill, which was at 2C. The horizontal line near the top of each graph represents viability estimated by tetrazolium for each collection.

suggests the possibility of using older seed for spring planting, when conditions for adequate stratification are less reliably present.

In a practical sense, the behavior of seed that is inadequately stratified is important, because field conditions may not be optimal for stratification. The effects of freezing, drying, and periods of warm temperature on inadequately stratified seed could affect the number of seeds available for germination at the appropriate time and might also affect their degree of dormancy. Young and Evans (1976) reported that the required stratification period was increased by moisture stress and that temperatures much below freezing were not effective for breaking dormancy. We have data to show that inadequately stratified seeds exposed to warm periods enter some type of secondary dormancy (Meyer and Monsen unpublished data at Provo, Utah). The effect of two two-week stratification periods broken by a week-long warm period was not additive; the warm-treated seeds apparently had to begin the stratification process anew. Similar induction of secondary dormancy has been reported for certain Russian tree seeds (Nikolaeva 1969). Source differences in response to these types of stress may be of adaptive significance in different types of habitats, but no clear patterns have emerged.

Rubber Rabbitbrush (Chrysothamnus nauseosus [Pall] Britton)

Range management interest in rubber rabbitbrush has more often been in the context of control than of encouragement through artificial seeding. But some races can provide valuable winter forage for big game within a short time of seeding. Rubber rabbitbrush has become a more prominent component of seeding mixes for winter game range restoration in recent years (Monsen and Stevens 1987).

Perhaps because of its generally low priority as a forage species, rubber rabbitbrush has received little attention in the germination literature. Papers by Kay et al. (1977) and Sabo et al. (1979) are among the few published accounts. In contrast, recent germination work in our laboratory has concentrated on this species, which presents a wide array of ecotypes from hot desert to subalpine communities (Anderson 1986).

Rubber rabbitbrush seed has generally been considered nondormant even when fresh (Dietschman et al. 1974). Our results have confirmed this observation. Seed from all sources tested germinated completely within a month at temperatures of 25C or 30C. (Meyer and McArthur 1987). Examination of germination totals at optimum temperatures would lead to the conclusion that source differences are unimportant. But dormancy is not the only adaptive option open to seeds. For fall-produced seeds like rubber rabbitbrush, the simple mechanism of controlling germination rate at cold temperatures accomplishes much the same end as dormancy in a summer-produced seed. The germination rate of rubber rabbitbrush seed at slightly-above-freezing temperatures varies dramatically from source to source.

Moreover, these source difference are correlated with climate parameters at the site of seed origin. Collections from sites with severe winters took as long as 100 days to reach 50% relative germination at 3C, while Mojave Desert sources germinated to 50% in less than a week (McArthur et al. 1987). Germination rate in the cold is negatively correlated with frost risk to seedlings germinating in the cold at the site of seed origin.

Rubber rabbitbrush seed is short-lived in dry storage and is probably not persistent in the seedbank under field conditions (Stevens et al. 1981; Meyer and McArthur 1987). Its seed germination pattern is predictive, using soil temperature cues to time germination appropriately in the months following seed production. Seeds from different habitat types read the temperature cues in a manner which minimizes seedling risk in each habitat type.

Big Sagebrush (Artemisia tridentata Nutt.)

Big sagebrush is a landscape dominant over vast acreages in the western United States and has received considerable research attention (McArthur and Plummer 1978; Harniss et al. 1981). The emphasis in the management literature has been on control, however, and there are relatively few germination studies. Much of the earlier work was carried out before the taxonomic complexity of the species was unravelled, which somewhat limits its usefulness. These early workers established the general nature of the big sagebrush germination syndrome (Shepherd 1937; Goodwin 1956; Payne 1957; Weldon et al. 1959). The seed was found to germinate rapidly, often within a few days, over a wide temperature range. Light consistently enhanced germination. Source differences in final germination percentages were found by Payne (1957) but the germination percentages are hard to interpret without some independent measure of total seed viability. This problem is common to all the early work and much of the later work as well.

McDonough and Harniss (1974a) were the first to look at between-subspecies differences in germination. They found that a Dubois, Idaho, collection of mountain big sagebrush (ssp. vaseyana) responded to 30-day prechill by increasing from 18% to 94% germination, while collections of Wyoming big sagebrush (ssp. wyomingensis) and basin big sagebrush (ssp. tridentata) from the same area showed the same intermediate germination percentages regardless of prechill. The viability of ungerminated seeds was not reported. Further studies of the dormancy of the mountain big sagebrush collection (McDonough and Harniss 1974b) revealed that the only dormancy-breaking treatment other than prechill which resulted in any substantial increase in germination percentage over the control was embryo excision. Naked embryos germinated to 95% within 24 hours.

Harniss and McDonough (1976) found significant year-to-year differences in germination of

Dubois basin big sagebrush seed but not in the other two subspecies. These differences could reflect differences in viability or in dormancy.

Young and Evans (1986) reported what they considered to be surprisingly little year-to-year variation in germination percentages for two mountain big sagebrush and three basin big sagebrush sources from western Nevada. Germination percentages at moderate temperatures were significantly lower for the mountain than for the basin big sagebrush collections (48% and 69% versus 75%, 83%, and 86%), but the extreme dormancy found in the Dubois source was lacking. Further, none of the western Nevada sources responded to prechill.

Harvey (1981) reported no dormancy in either mountain big sagebrush or Wyoming big sagebrush seed and no differences between sources or between collection years either in response to temperature or in total germination percentages. Harvey claimed that the low germination percentages obtained by earlier workers were due to 'auto-inhibition' caused by crowding too many seeds into the enclosed volume of a petri dish. The auto-inhibition was credited to volatile and/or water-soluble inhibitors which needed to diffuse away before germination could take place. When this problem was alleviated by germinating the seeds on an open thermogradient bar, he obtained uniformly high germination percentages.

Work on source differences in big sagebrush germination is currently underway in our laboratory. Some preliminary results are given in Table 3. In an experiment with fresh 1986 seed at 15C with a 12-hour photoperiod, germination rate varied both among subspecies and within subspecies. Basin big sagebrush collections germinated fastest, Wyoming big sagebrush collections germinated at an intermediate rate, and mountain big sagebrush collections germinated slowest, overall. Within-subspecies variation was especially marked in the mountain big sagebrush collections, with relatively low elevation collections such as Little Sahara Cutoff and Utah Hill germinating fastest and high elevation sources such as Nebo Overlook and Huntsville germinating slowest. Experience with rubber rabbitbrush suggests that rate differences at colder temperatures will represent a magnified version of these differences, but data are not yet available to test that hypothesis. Only two sources, the slowest mountain big sagebrush collections, contained more than 5% dormant seed at the end of the 30-day test.

Like rubber rabbitbrush, big sagebrush produces seed in the autumn and early winter, and the seeds have a relatively short tenure in the soil (Mueggler 1956; Young and Evans 1975). A predictive germination pattern like the pattern in rubber rabbitbrush would therefore not be unexpected, though the possibility of autopathy through chemical inhibition adds a somewhat different dimension.

Table 3. Relative germination percentages at day 3, day 7 and day 15 for 18 fresh big sagebrush collections belonging to three subspecies. Seeds were germinated in four replications of 25 seeds at 15C with a 12-hour photoperiod. Percentages are based on germinated plus dormant seed at the end of the 30-day test.

Source	Day 3	Day 7	Day 15
ssp. tridentata			
Big Pine, CA	98	100	100
Moab, UT	90	99	100
Stagecoach, NV	83	96	100
Oak City, UT	84	100	100
Ely, NV	66	99	100
Tahoe Jct., NV	58	96	100
ssp. wyomingensis			
Parowan Gap, UT	83	100	100
Oasis, NV	68	97	100
Golconda Summit, NV	66	97	100
Blanding, UT	63	97	100
Cedar Ft., UT	13	75	99
Kemmerer, WY	9	77	96
ssp. vaseyana			
Utah Hill, UT	56	98	100
Lt. Sahara Cutoff, UT	37	90	100
LeeVining, CA	23	68	97
Wheeler Station, CA	9	63	93
Nebo Overlook, UT	2	22	60
Huntsville, UT	0	20	69

TACTICS FOR STUDIES ON BETWEEN-POPULATION VARIATION

Studies specifically aimed at characterizing between-population variation in germination patterns in relation to habitat differences can yield rapid and satisfying results as long as models are kept simple and a sufficient number of sources are included. The 'noise' created by non-average conditions during ripening is seen in better perspective when many sources are examined. These kinds of experiments are practical because only a few treatments are necessary in order to detect relevant source differences.

When characterizing germination patterns at the population level, it is important to collect from a sufficient number of individuals to obtain a reasonable estimate of the mean response for the population as a whole. Collecting from individual plants represents research at another level of infraspecific variation.

The problem of distinguishing between differences in seed viability and differences in germinability of viable seed is particularly acute in multi-source experiments, because viability differences between sources can effectively mask differences in germination response. It is important to have some independent measure of percent viability and to express the results of germination tests on a percent-viable-seed basis before attempting correlations. Independent viability measures include treatments known to break dormancy completely for all lots, a tetrazolium viability test on a comparable subsample, or a tetrazolium test or at least a cut test on ungerminated seeds left at the end of the germination period (AOSA 1984).

RESEARCH DIRECTIONS AND APPLICATIONS

Understanding the relationship between germination patterns and habitat characteristics could be immediately useful in the context of range seeding and management of natural stands. Predictive indices such as low temperature germination rate or germination percentage after incomplete stratification could be used to predict the probability of establishment success on particular sites, especially for commercial lots of unknown provenance.

Once the genetic and environmental components of interpopulation variation have been partitioned through common garden techniques, the possibility of creating seed sources with desirable combinations of establishment traits will exist. If the major component for the desirable trait is genetic, standard plant selection and breeding techniques could be applied.

If, as seems more likely at this time, the trait is controlled largely by conditions during seed maturation, then seed germination patterns could be manipulated by planting seed orchards at sites which will induce the desired response. For example, sources with inherent frost tolerance might be induced to produce seeds which germinate rapidly in the cold if planted at lower-elevation sites. These seeds would have an immediate advantage in competition with early-emerging exotic annuals or with aggressive grasses and forbs in an artificial seeding mix, yet would produce progeny with germination traits tailored to natural conditions at the planting site, whatever its climate. Clearly there are other factors affecting long-term survival of an ecotype on a particular site, but if the principal need is to produce early-emerging, frost-tolerant seedlings, this might be a way to achieve it.

More laboratory studies are needed to determine whether interpretable patterns of infraspecific variation in germination behavior exist for other important range species, and to investigate the causes of such variation. At least as important is the initiation of field establishment trials using different sources of known traits on different site types. Only in this way can we learn whether the predictive indices developed in the laboratory have any validity in the field.

LITERATURE CITED

Alderfer, J. 1976. A taxonomic study of bitterbrush (Purshia tridentata [Pursh] DC. in Oregon. M.S. thesis. Oregon State University, Corvallis, Oregon.

Allen, P. A., S. E. Meyer, and T. D. Davis. 1987. Determining seed quality of winterfat (Ceratoides lanata [Pursh] J. T. Howell). J. Seed Tech. (In press).

Anderson, L. C. 1986. An overview of the genus Chrysothamnus (Asteraceae). In: E. D. McArthur and B. L. Welch (compilers). Proc.-- Symposium on the Biology of Artemisia and Chrysothamnus. USFS Gen. Tech. Rep. INT-200. p. 29-45.

AOSA. 1984. Rules for testing seeds. 1984 revision. J. Seed Tech. 6:1-126.

Barnes, B. V. 1967. Phenotypic variation associated with elevation in western white pine. For. Sci. 13:357-364.

Basile, J. V. 1967. An annotated bibliography of bitterbrush (Purshia tridentata [Pursh] DC). USFS Res. Pap. INT-44.

Clark, L. D., and N. E. West. 1971. Further studies of Eurotia lanata germination in relation to salinity. Southwestern Nat. 15:371-375.

Cresswell, E. G., and J. P. Grime. 1981. Induction of a light requirement during seed development and its ecological consequences. Nature 291:583-585.

Crofts, K. A. 1977. The importance of utricle-related factors in germination and seedling vigor of four species of perennial Atriplex. M.S. thesis. Utah State University, Logan, Utah.

Davis, J. N. 1983. Performance comparisons among populations of bitterbrush, cliffrose, and bitterbrush-cliffrose crosses on study sites throughout Utah. In: A. R. Tiedemann and K. L. Johnson (compilers). Proc.--Research and management of bitterbrush and cliffrose in western North America. USFS Gen. Tech. Rep. INT-152. p. 38-44.

Dettori, M. L., J. F. Balliete, J. A. Young, and R. L. Evans. 1984. Temperature profiles for germination of two species of winterfat. J. Range Manage. 37:218-222.

Dietschman, G. H., K. R. Jorgensen, and A. P. Plummer. 1974. Chrysothamnus. In: C. S. Schopmeyer (ed.). Seeds of woody plants in the United States. USDA Handbook No. 450. p. 326-328.

Evans, R. L., and J. A. Young. 1977. Bitterbrush germination with constant and alternating temperatures. J. Range Manage. 30:30-32.

Evans, R. A., J. A. Young, G. J. Cluff, and J. K. McAdoo. 1983. Dynamics of antelope bitterbrush seed caches. In: A. R. Tiedemann and K. L. Johnson (compilers). Proc.--Research and management of bitterbrush and cliffrose in western North America. USFS Gen. Tech. Rep. INT-152. p. 195-202.

Everett, R. L., and R. O. Meeuwig. 1978. Hydrogen peroxide and thiourea treatment of bitterbrush seed. USFS Res. Note INT-196.

Everett, R. L., R. O. Meeuwig, and R. Stevens. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. J. Range Manage. 31:70-73.

Fenner, M. 1985. Seed ecology. Chapman and Hall, London and NY.

Gamrath, W. G. 1972. The relationship of plant morphology and seed processing to utricle fill and germination of fourwing saltbush (Atriplex canescens [Pursh] Nutt.). M.S. thesis. Montana State University, Bozeman, Montana.

Gerard, J. B. 1978. Factors affecting fruit fill and seed germination of fourwing saltbush (Atriplex canescens [Pursh] Nutt.). Proc. First International Range Conference. Society for Range Management, Denver, Colorado. p. 403-405.

Giunta, B. C., R. Stevens, K. R. Jorgensen, and A. P. Plummer. 1978. Antelope bitterbrush--an important wildland shrub. Utah State Div. of Wildlife Resources Pub. No. 78-12.

Goodwin, D. L. 1956. Autecological studies of Artemisia tridentata. Ph.D. dissertation. Washington State University, Pullman.

Gutterman, Y. 1980. Influences on seed germinability: phenotypic maternal effects during seed maturation. Isr. J. Bot. 29:105-117.

Harniss, R. O., and W. T. McDonough. 1976. Yearly variation in germination in three subspecies of big sagebrush. J. Range Manage. 29:167-168.

Harniss, R. O., S. J. Harvey, and R. B. Murray. 1981. A computerized bibliography of selected sagebrush species (genus Artemisia) in western North America. USFS Gen. Tech. Rep. INT-102.

Harper, J. L., and I. H. McNaughton. 1960. The inheritance of dormancy in inter- and intra-specific hybrids of Papaver. Heredity (London) 15:315-320.

Harper, L. W. 1970. The use of thiourea for laboratory testing of antelope bitterbrush seed. Proc. AOSA 60:127-131.

Harvey, S. J. 1981. Life history and reproductive strategies in Artemisia. M.S. thesis. Montana State University, Bozeman.

Hilton, J. W. 1941. Effects of certain microecological factors on the germinability and early development of Eurotia lanata. Northwest Science 15:86-92.

Hormay, A. L. 1943. Bitterbrush in California. Forest Research Note No. 34. California Forest and Range Experiment Station.

Johnson, W. J. 1975. Factors affecting utricle fill in fourwing saltbush (Atriplex canescens [Pursh] Nutt.). M.S. thesis. Montana State University, Bozeman.

Kay, B. L., C. M. Ross, and W. L. Graves. 1977. Rubber rabbitbrush. University of California-Davis Agronomy and Range Science Mojave Revegetation Notes No. 3.

Koller, D. 1972. Environmental control of seed germination. In: T. T. Kozlowski (ed.). Seed biology. Vol. II. Academic Press, NY. p. 2-101.

McArthur, E. D., A. C. Blauer, A. P. Plummer, and R. Stevens. 1979. Characteristics and hybridization of important Intermountain shrubs. III. The sunflower family. USDA Forest Service Res. Pap. INT-220.

McArthur, E. D., S. E. Meyer, and D. J. Weber. 1987. Germination rate at low temperature: rubber rabbitbrush population differences. J. Range Manage. (In press).

McArthur, E. D., and A. P. Plummer. 1978. Biogeography and management of native western shrubs: A case study, section Tridentatae of Artemisia. Great Basin Natur. Mem. 2:229-243.

McConnell, B. R. 1960. Effect of gibberellic acid and cold treatments on the germination of bitterbrush seed. USFS Res. Note 187. Pacific Northwest Forest and Range Experiment Station.

McDonough, W. T., and R. O. Harniss. 1974a. Effects of temperature on germination in three subspecies of big sagebrush. J. Range Manage. 27:204-205.

McDonough, W. T., and R. O. Harniss. 1974b. Seed dormancy in Artemisia tridentata ssp. vaseyana Rydb. Northwest Science 48:17-20.

McHenry, W. B., and L. A. Jensen. 1967. Response of bitterbrush (Purshia tridentata) seed to certain germination methods. Proc. AOSA 57:89-95.

Meyer, S. E., P. A. Allen, G. R. Wilson, T. D. Davis, J. N. Davis, R. Stevens, and K. Jorgensen. 1986. Proposed rule for antelope bitterbrush--*Purshia tridentata*. AOSA Newsletter 69(1):21-22.

Meyer, S. E., and E. D. McArthur. 1987. Studies on the seed germination biology of rubber rabbitbrush. In: K. L. Johnson (ed.). Proc. Fourth Utah Shrub Ecology Workshop. Utah State University, Logan. (In press).

Monsen, S. B., and J. N. Davis. 1985. Progress in the improvement of selected western North American Rosaceous shrubs. In: J. R. Carlson and E. D. McArthur (eds.). Symposium on range improvement in western North America. Soc. for Range Manage., Denver, Colorado. p. 201-209.

Monsen, S. B., and E. D. McArthur. 1985. Factors influencing establishment of seeded broadleaf herbs and shrubs following fire. In: K. Sanders and J. Durham (eds.). Rangeland fire effects: A symposium. USDI Bureau of Land Management, Idaho State Office, Boise. p. 112-124.

Monsen, S. B., and R. Stevens. 1987. Seed and seeding characteristics of rubber rabbitbrush. In: K. L. Johnson (ed.). Proc. Fourth Utah Shrub Ecology Workshop. Utah State University, Logan. (In press).

Morley, F. H. W. 1958. The inheritance and ecological significance of seed dormancy in subterranean clover (*Trifolium subterraneum* L.) Aust. J. Biol. Sci. 11:261-274.

Moyer, J. L., and R. L. Lang. 1975. Variable germination response to temperature for different sources of winterfat seed. J. Range Manage. 29:320-321.

Mueggler, W. F. 1956. Is sagebrush seed residual in soil or is it wind borne? USFS Res. Note No. 35. Intermountain Forest and Range Experiment Station.

Neal, D. L., and H. R. Sanderson. 1975. Thiourea solution temperature and bitterbrush germination and seedling growth. J. Range Manage. 28:421-423.

Nikolaeva, M. G. 1969. Physiology of deep dormancy in seeds. Israel Program for Scientific Translations, Ltd. Jerusalem, Israel. (Translated from Russian).

Nord, E. C. 1956. Quick testing bitterbrush seed viability. J. Range Manage. 9:193-194.

Nord, E. C., and J. E. Whitacre. 1957. Germination of fourwing saltbush seed improved by scarification and grading. USFS Res. Note No. 125. California Forest and Range Experiment Station.

Payne, G. F. 1957. Some germination studies of *Artemisia tridentata*. Proc. Montana Acad. Sci. 17:41-42.

Pearson, B. O. 1957. Bitterbrush seed dormancy broken with thiourea. J. Range Manage. 10:41-42.

Plummer, A. P., S. B. Monsen, and D. R. Christensen. 1966. Fourwing saltbush a shrub for future game ranges. Utah State Dept. Fish and Game Pub. No. 66-4.

Plummer, A. P., D. R. Christensen, and S. B. Monsen. 1968. Restoring big game range in Utah. Utah State Dept. Fish and Game Pub. No. 68-3.

Reidl, W. A., K. H. Asay, J. L. Nelson, and G. M. Telwar. 1964. Studies of *Eurotia lanata* (winterfat). Wyo. Agric. Exp. Stat. Bull. 425.

Sabo, D. G., G. V. Johnson, W. C. Martin, and E. F. Aldon. 1979. Germination requirements of 19 species of arid land plants. USFS Res. Pap. RM-210.

Shepherd, W. O. 1937. Viability and germination characteristics of sagebrush. M.S. thesis. Utah State University, Logan.

Silvertown, J. W. 1984. Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. Amer. Natur. 124:1-16.

Springfield, H. W. 1964. Some factors affecting germination of fourwing saltbush. USFS Res. Note RM-25.

Springfield, H. W. 1966. Germination of fourwing saltbush seeds at different levels of moisture stress. Agron. J. 58:149-150.

Springfield, H. W. 1968a. Age and year of collection affect germination of winterfat seeds. USFS Res. Note RM-112.

Springfield, H. W. 1968b. Germination of winterfat seed under different moisture stresses and temperatures. J. Range Manage. 21:314-316.

Springfield, H. W. 1968c. Cold storage not required for fourwing saltbush seeds. J. Range Manage. 21:335-336.

Springfield, H. W. 1969. Temperatures for germination of fourwing saltbush. J. Range Manage. 22:49-50.

Springfield, H. W. 1970. Germination and establishment of fourwing saltbush in the Southwest. USFS Res. Pap. RM-55.

Springfield, H. W. 1972a. Winterfat seeds undergo afterripening. J. Range Manage. 25:479-480.

Springfield, H. W. 1972b. Optimum temperatures for germination of winterfat. J. Range Manage. 25:69-70.

Springfield, H. W. 1973. Larger seeds of winterfat germinate better. J. Range Manage. 26:153-154.

Stearns, R., and J. Olsen. 1958. Interaction of photoperiod and temperature affecting germination in Tsuga canadensis. Am. J. Bot. 45:53-58.

Stevens, R., B. C. Giunta, K. R. Jorgensen, and A. P. Plummer. 1977. Winterfat. Utah State Div. of Wildlife Resources Pub. No. 77-2.

Stevens, R., K. R. Jorgensen, J. N. Davis. 1981. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage. Great Basin Nat. 41:274-277.

Stutz, H. C., C. L. Pope, and T. Leslie. 1975. Germination studies of Atriplex. In: Wildland shrubs, symposium and workshop proceedings on the occasion of the dedication of the USFS Shrub Sciences Laboratory, Provo, Utah. p. 150.

Twitchell, L. T. 1955. Germination of fourwing saltbush as affected by soaking and chloride removal. J. Range Manage. 8:218-220.

Weldon, L. W., D. W. Bohmont, and H. P. Alley. 1959. The interrelation of three environmental factors affecting germination of sagebrush seed. J. Range Manage. 12:236-238.

Wilson, C. P. 1928. Factors affecting the germination and growth of chamiza (Atriplex canescens). New Mexico Agri. Expt. Sta. Bull. 169.

Witcomb, J. R., and W. J. Whittington. 1972. The effects of selection for reduced dormancy in charlock. Heredity 29:37-41.

Workman, J. P., and N. E. West. 1967. Germination of Eurotia lanata in relation to temperature and salinity. Ecology 48:659-661.

Young, J. A., and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. Weed Sci. 23:358-364.

Young, J. A., and R. A. Evans. 1976. Stratification of bitterbrush seeds. J. Range Manage. 29:421-425.

Young, J. A., and R. A. Evans. 1981a. Germination of Great Basin Wildrye seeds collected from native stands. Agron. J. 73:917-920.

Young, J. A., and R. A. Evans. 1981b. Germination of seeds of antelope bitterbrush, desert bitterbrush, and cliffrose. USDA Science and Education Administration ARR-W-17/January 1981.

Young, J. A., and R. A. Evans. 1986. Germination profiles for five populations of big sagebrush. In: E. D. McArthur and B. L. Welch (compilers). Symposium on the biology of Artemisia and Chryosthamnus. USFS Gen. Tech. Rep. INT-200. p. 370-374.

THE SIMULATION OF SOIL TEMPERATURE AND WATER
REGIMES ASSOCIATED WITH SEEDLING ESTABLISHMENT ON
RANGELAND SOILS

J. Ross Wight and Clayton L. Hanson

ABSTRACT

Problems associate with modeling the soil
temperature and water regimes in the soil layer
associated with seedling etablishment and the
utility of models such as SPUR and ERHYM for these
purposes are discussed. Preliminary studies
indicate that such models will need some
modification before they can be used effectively
for this purpose. Also, the use of long-term
simulated data to calculate probability of
occurrences of environmental conditions favorable
for seedling establishment is demonstrated.

INTRODUCTION

Plant recruitment is a continuous process in
rangeland ecosystems. It is a controlling factor
in the productivity of annual grasslands and in
the establishment of seeded pasture. Recruitment
also plays a major role in primary and secondary
succession in perennial grasslands.

The environmental requirements for seed
germination have been studied extensively for most
agriculture crops and many range plants. Studies
such as reported by Young and Evans (1982) are
major sources of this type of information for
native range plants. To relate the results of
laboratory germination studies to field conditions
and seedling establishment, the seedling
environment must be characterized as is done in
studies such as those reported by Evans et al.
(1975). Soil temperature and water are the
primary environmental factors associated with seed
germination and seedling etablishment of native
and exotic plant species. Soil temperature is
easily measured and recorded with a variety of
available data recording systems. Continuous
recordings of soil water content or, more
importantly, soil water tension is much more
difficult because sensors are not available to
cover the entire range of soil water conditions
found in the surface layer.

Annual climates and the associated soil water and
soil temperature regimes are highly variable. The
seedling environment is further affected by such
factors as soil texture, site slope, and surface
cover. It is not practical to try to classify
seedling environments for the wide range of sites
associated with rangelands. Thus it is important
to be able to simulate seedling environments based
on climatic data such as maximum and minimum air
temperatures and precipitation and site
characteristics. Such simulations are necessary
in the development of plant recruitment and plant
succession models. Simulation also provides a
means of developing a long-term record from which
probabilities of occurrence of specific
environmental conditions can be calculated.

[1]Range Scientist and Hydrologist , USDA-ARS,
270 S. Orchard, Boise, ID 83705

Most soil temperature and water models have been
developed for application to croplands and often
require fairly intensive climatic inputs. The
rangeland models SPUR (Wight 1983) and ERHYM
(Wight 1987) have soil temperature and water
submodels that are driven by maximum and minimum
temperatures, solar radiation and precipitation.
These submodels were not designed for nor have
they been tested for simulating soil temperature
and water content in the soil layer associated
with seed germination and seedling establishment.
A major problem in developing and testing models
for simulating soil water dynamics in this soil
layer is the lack of field data.

This paper discusses some of the problems and
concerns relative to modeling the temperature and
water regimes of the soil layer associated with
seed germination and seedling establishment. Also
discussed is the utility of simulated soil
temperature and water data for calculating
probabilities of occurrences of specific soil
temperature-water regimes which can be used to
predict seedling establishment.

RESULTS AND DISCUSSIONS

Soil temperature models such as used in EPIC
(Williams et al. 1982), which is currently used in
ERHYM, were designed to simulate soil temperatures
in the root zone. Soil temperature simulations
using ERHYM indicate such models become less
reliable as the simulation depth approaches the
soil surface. The greatest discrepancies occurred
in the summer months when soil surface
temperatures were as much as 15 to $20^{\circ}C$ higher
than the air temperatures. In early spring, at
the beginning of the growing season, and in fall,
prior to killing frosts (the cooler portions of
the growing season), simulated soil temperatures
within 2.5 cm of the soil surface were closely
related to actual field values. By adding a
function to account for the discrepancies during
the summer months, ERHYM was able to simulate soil
temperatures within 2.5 cm of the soil surface
with reasonable accuracy.

Models are often judged by their ability to
simulate accurately and their ease of use, which
are usually inversely related. A first step in
developing or choosing a model is to determine
what level of accuracy is needed. Soil
temperature and water models usually consider only
one point or profile within a field or range site
without regard to the inherent spatial variability
within a field or site. In validating a model for
practical applications, spatial variability should
be considered.

The spatial variability of soil characteristics
such as soil temperature and soil water content is
receiving increasing attention in terms of the
magnitude of the variability; interdependency of
observations and how to describe those
interrelationships; and how to handle this
variability in terms of spatial modeling. For
soil surface temperatures measured along an 80-m
transect over bare soil, Davidoff et al. (1986)

reported a coefficient of variation (CV) of 9.35 and a range of 6.8°C around a mean of 18.38°C. At the 5-cm depth, the CV and range were 5.48 and 4.7°C, respectively, around a mean of 16.44°C. Higher variation would be expected during the hot summer temperatures and on rangelands with variable amounts of litter and plant cover.

Another important consideration in modeling soil temperature is the temporal variability. Many root-zone temperature models are concerned only with the daily means. Such is the case in SPUR and ERHYM. For seed germination, the daily maximum and minimum temperatures and the magnitude of the difference between the maximum and minimum are important. The soil temperature model in ERHYM uses the daily mean air temperature as a driver. By using daily maximum air temperature as the driver, the model was able to simulate maximum soil temperature with about the same accuracy as it simulated the mean. Using minimum air temperature, minimum soil temperature was simulated but with a little less accuracy.

The soil temperature model in ERHYM simulates daily soil temperature based on the long-term average air temperature, current day's air temperature, the previous day's soil temperature, and soil water and bulk density. For the soil surface and near surface depths, air temperature, insolation, soil water, and albedo are the major factors. For rangeland conditions, canopy shade and ground cover also are important. There are two soil temperature models similar to that used in ERHYM that include functions to account for insolation and albedo (Jones et al. 1986) and cover (Arnold et al. 1987).

Soil water models such as those used in SPUR (Ritchie 1972) and ERHYM were designed to simulate soil water content of soil layers within the root zone. Their ability to simulate the soil water content in the surface 2 cm has not been evaluated. For soil surface layers of greater thickness, soil water models have performed reasonably well. Saxton showed good agreement between field-measured and model-predicted soil water values for the surface 7.6 cm layer using the SPAW model (Saxton 1985). The ERHYM model simulated the soil water content of a 15 cm surface layer on a range site in Central Wyoming with reasonable accuracy (Wight et al. 1986).

Again there is a question of what is reasonable accuracy. What should the goals be in modeling soil water? Spatial variability is a major concern. Variability in the surface few centimeters of soil on rangelands can be considerable due to the microrelief and variable plant and litter cover. Hunter and Greger (1986) found that soil moisture measured by resistance blocks placed 2 to 4 cm apart varied by as much as 8 percentage units of volumetric water. In plots with the vegetation removed, the variation was only 2 percentage units, indicating that most of the variation was due to spatial variability.

Spatial and temporal variation of soil water within the profile is also important. Following a light rain on a dry soil, favorable soil water conditions may persist long enough at the surface to permit seed germination but soil water is inadequate to support root growth and seedling establishment.

PROBABILITY OF OCCURRENCE

To calculate probabilities of occurrence of specific environmental conditions such as soil temperature regimes, long-term simulations of soil temperature are needed. Such simulations require climatic records of similar length. Where long-term climatic records are not available, they can often be provided by using a stochastic climatic generator. In this example we used the climate subroutine in SPUR (Hanson and Richardson 1983) to generate a 50-year climate record for the Reynolds Creek Experimental Watershed. The mean values for the 50-year generated record were then compared with 27 years of actual climatic data.

The mean monthly precipitation, maximum and minimum temperature, and solar radiation of the generated data were in close agreement with those from the actual climate record (Tables 1, 2, and 3). None of the mean monthly precipitation values was more than 13 percent different from the measured values except August where the difference was 15 percent. The mean monthly generated maximum and minimum temperatures were all within 3°C of the measured values with no seasonal differences. The annual means of the measured and generated, maximum and minimum temperatures were the same. The generated solar radiation values were generally lower than the observed during the winter months and greater during the summer with the annual means being within 4 percent.

Table 1. Average monthly precipitation (mm) and number of wet days from data generated by SPUR and from observed data from Reynolds Creek, ID.

Month	Precipitation		Number of wet days	
	Observed	Generated	Observed	Generated
Jan	33	33	10.9	10.7
Feb	23	21	9.5	9.1
Mar	25	23	10.2	9.8
Apr	25	27	8.1	8.3
May	22	23	8.0	8.3
June	31	35	7.7	8.7
July	8	8	3.0	3.4
Aug	18	21	4.7	4.8
Sept	16	17	4.2	4.5
Oct	19	19	6.2	6.4
Nov	33	35	10.8	11.6
Dec	34	34	11.5	11.4
Annual	287	296	94.9	97.2

Table 2. Mean daily maximum and minimum
temperatures (^{O}C), and solar
radiation (Langleys) by month
for data generated by SPUR and
from observed data from Reynolds
Creek, ID.

| Month | Temperature | | | | Solar | |
| | Maximum | | Minimum | | Radiation | |
	[1]Obs	Gen	Obs	Gen	Obs	Gen
Jan	3	2	-6	-6	167	131
Feb	6	3	-4	-5	255	220
Mar	9	8	-3	-3	364	344
Apr	13	14	0	1	493	502
May	19	21	4	5	586	612
June	24	27	8	9	646	654
July	29	29	12	10	650	656
Aug	29	27	11	9	567	555
Sept	22	23	6	6	449	416
Oct	16	16	1	2	315	276
Nov	8	8	-3	-2	180	142
Dec	3	4	-6	-5	148	106
Mean	15	15	2	2	401	385

[1]Obs = Observed; Gen = Generated

Table 3. Maximum and minimum annual
precipitation, mean annual number of
wet days, and the maximum and minimum
temperatures generated by SPUR and
observed at Reynolds Creek, ID.

Variable	Observed	Generated
Maximum annual precip. (mm)	370	402
Minimum annual precip. (mm)	175	200
Mean annual number of wet days	63	78
Maximum temperature (^{O}C)	39	41
Minimum temperature (^{O}C)	-29	-23

The generated climatic record was used to drive
the ERHYM model to obtain a 50-year record of
daily maximum and minimum soil temperatures.
Young and Evans (1982) reported that for several
grass species, maximum germination was when the
daily maximum temperature was about 20°C and
minimum temperature was about 15°C. From the
simulated soil temperature record, we identified
the time periods in the spring and fall of each
year when the temperature regime was most
favorable for seed germination. Analysis of these
data indicate that for this range site the most
favorable soil temperature regime for seed
germination would occur 90 percent of the time
during late April and early May in the spring and
64 precent of the time during the first two weeks
of September in the fall (Table 4). This soil
temperature information could be combined with the
soil water model information to obtain a more
realistic estimate of the time of optimum
germination.

Table 4. Periods favorable for seed
germination and their probabilities
of occurrence based on soil
temperatures at Reynolds Creek, Idaho.

Spring Germination	April	1-15	.08
	April	16-30	.58
	May	1-15	.32
	May	16-31	.02
Fall Germination	Aug	15-31	.12
	Sept	1-15	.64
	Sept	16-30	.24

SUMMARY

Simulation of the soil temperature and water
regimes associated with seed germination and
seedling establishment is important in the
development of recruitment models and
understanding of plant community dynamics. The
soil temperature routines in the rangelands models
SPUR and ERHYM were not designed for simulating
soil temperature in the surface few centimeters.
Preliminary tests indicate that they will probably
need some modification before they can be used
effectively for this purpose. Algorithms for
such modification have been developed (Jones et
al. 1986; Arnold et al. 1987).

Simulation of the soil water regimes in the upper
2 to 3 cm of the soil surface is a more complex
problem. This layer of soil dries very rapidly,
but water moves to the surface from subsurface
layers by both capillary action and vapor
movement. The water regime in the surface few
centimeters of soil is a dynamic process, and the
simulation of its dynamics is beyond the scope of
either SPUR or ERHYM. However, such detailed
simulations may not be necessary for practical
application in characterizing the seedling
environment. The soil water models in SPUR and
ERHYM both provide good simulations of soil water
content in soil layers of 15 or more cm. They
have not been tested for small increments of
profile near the soil surface, and data for such
testing is generally not available.

Also important in modeling soil temperature and
water in the soil surface layer is the magnitude
of spatial variability and its relationship to the
modeling objectives.

LITERATURE CITED

Arnold, J. G., J. R. Williams, and A. D. Nicks.
1987. SWRRB-A basin scale simulation model
for soil and water resource management, Texas
A&M Press, College Station. (In Press)

Davidoff, B., J. W. Lewis, and H. M. Selim. 1986.
Variability of soil temperature with depth
along a transect. Soil Science 142:114-122.

Evans, R. A., B. L. Kay, and J. A. Young. 1975.
Microenvironment of a dynamic annual community
in relation to range improvement. Hilgardia
43:79-102.

Hanson, C. L. and C. W. Richardson. 1983. SPUR
Climate Component, pp. 5-16 In J. Ross Wight
(ed.), SPUR--Simulation of Production and
Utilization of Rangelands: A Rangeland Model
for Management and Research. USDA-ARS
Miscellaneous Publication number 1431:5-16.

Hunter, Richard and Paul D. Greger. 1986. Desert
water balance using a combination of
psychrometric and resistance sensors. In
Leonard J. Lane (ed.), Erosion on Rangelands:
Emerging Technology and Data Base. Proc. of
the Rainfall Simulator Workshop, January
14-15, 1985, Tucson, AZ. Society for Range
Management, Denver: p. 20-34.

Jones, C. A., J. T. Ritchie, J. R. Kiniry, and D.
C. Godwin. 1986. Subroutine structure. In
C. A. Jones, and J. R. Kiniry (eds.),
CERES-MAIZE, A Simulation Model of Maize
Growth and Development, Texas A&M Press,
College Station: p. 49-111.

Ritchie, J. T. 1972. A model for predicting
evaporation from a row crop with incomplete
cover. Water Resour. Res. 8:1204-1213.

Saxton, K. E. 1985. Soil water hydrology:
Simulation for water balance computations. In
A. Van Der Beken and A. Herrmann (eds.) New
Approaches in Water Balance Computations,
Proc. of the Hamburg Workshop, August 1983,
IAHS Publ. No. 148, p. 47-59.

Wight, J. R. (ed.). 1983. SPUR--Simulation of
Production and Utiliation of Rangelands: A
Rangeland Model for Management and Research.
USDA Misc. Publ. 1431, 120 p.

Wight, J. Ross, Herbert G. Fisser, and Clayton L.
Hanson. 1986. Biology and ecology of
sagebrush in Wyoming: IV. Validation of a
rangeland production model (ERHYM) for
sagebrush sites. In: E. Durant McArthur;
Bruce L. Welch (compilers). Proceedings --
symposium on the biology of Artemisia and
Ehrysothamnus; 1984, July 9-13; Provo, UT:
U.S. Department of Agriculture, Forest
Service, Intermountain Research Station;
398 p.

Wight, J. Ross. 1987. ERHYM-II: Model
description and user guide for the BASIC
version. U.S. Department of Agriculture,
Agricultural Research Service, ARS-59, 23 p.

Williams, J. R., P. T. Dyke, and C. A. Jones.
1982. EPIC--A model for assessing the effects
of erosion on soil productivity. In W. K.
Lauenroth, G. V. Skogerbe, and M. Flug (eds.),
Analysis of Ecological Systems:
State-of-the-Art in Ecological Modelling.
Developments in Environmental Modelling 5.
Elsevier Scientific Publ. Co. 1983, p.
553-572.

Young, James A. and Raymond A. Evans. 1982.
Temperature profiles for germination of cool
season range grasses. USDA-ARS, Agricultural
Research Results, ARR-W-27, 92 p.

COMPARATIVE ANALYSIS OF TEMPERATURE - GERMINATION RESPONSE SURFACES

Debra E. Palmquist[1], Raymond A. Evans[2], and James A. Young[3]

ABSTRACT

Quadratic response surface analysis has been employed to analyze data of seed germination in relation to combinations of cold and warm temperatures. A method for multiple response surface comparisons was used to show whether overall differences existed between six representative species of the big sagebrush (Artemisia tridentata Nutt.) ecosystem. A multiple comparison technique, based on confidence intervals from the response surfaces, was used to locate differences in relation to biologically important germination/temperature regimes.

INTRODUCTION

The problems of inappropriate multiple comparison procedures for comparing treatment means of quantitative variables have been documented by Peterson (1977), Chew (1976), and others. Multiple regression techniques have been shown to be a statistically precise and valid method for comparing between levels of these quantitative factors (Evans et al. 1982).

Regression lines or surfaces are calculated from experimental data so that a model relating the measured response variable (dependent variable) to a set of variables thought to influence it (independent variables), may be derived. This model should give the experimenter a statistically reasonable approximation of the relationship between the variables even at those points where no experimental data was collected. Regression is a very good predictive tool for researchers working with variables, such as temperature, where interpolated values may be of interest. Once multiple regression techniques are employed to derive an equation, confidence intervals can then be used to statistically answer specific analysis-of-variance type questions about differences between treatment means, or to find statistical differences between any two, or more, points or areas described by the equation (Ott, 1977).

Comparisons between two or more regression equations of the same form would enable an experimenter to obtain information about the differences, if any, between the equations. Upon finding overall differences between the surfaces being studied, a technique for ascertaining where these differences occur would be most useful.

Separate quadratic response surfaces were developed for different plant species, relating germination percentages to constant and alternating combinations of cold and warm temperatures. For each surface, the corresponding confidence intervals were derived. This provided statistical information for comparisons between the effects of specific temperature combinations on germination within a species.

A method for multiple response surface comparisons will be demonstrated, showing whether or not overall differences between these plant species existed. A multiple comparison technique, based on the confidence intervals derived from the surfaces, will be shown and used to compare biologically important germination/temperature regimes between the plant species studied.

MATERIALS AND METHODS

Representative herbaceous species of big sagebrush communities were chosen for the study. The species were crested wheatgrass (Agropyron desertorum Fisch. ex Link., 'Nordan') a perennial often seeded to revegetate degraded big sagebrush communities (Young and Evans 1982); downy brome (Bromus tectorum L.) an introduced annual grass that is the seral dominant of millions of degraded big sagebrush hectares (Evans and Young 1972); Russian thistle (Salsola australis R. Br.), an introduced weed that is the first species to invade disturbed big sagebrush communities (Evans and Young 1982); barbwire Russian thistle (S. paulsenii Lit.) a recently introduced weed found on the margin of salt desert (Young and Evans 1979); tumble mustard (Sisymbrium altissimum L.) a broadleaf weed that replaces Russian thistle in a seral continium; and common mullein (Verbascum thapsus L.) a ruderal weed in the big sagebrush zone (Semenza et al, 1978).

The seeds from these six plant species were incubated for four weeks in dark germinators under a regime of 55 constant and alternating temperatures. Constant temperature regimes were 0, 2, 5, and at 5 degree increments through 40°C. Alternating temperature regimes consisted of 16 hours cold period and 8 hours warm period, at all possible higher temperatures for each 24 hour interval. For example, 2°C (cold period) was alternated with 5, 10, 15, 20, 25, 30, 35 and 40°C (warm period), and 30°C (cold period) was only alternated with 35°C and 40°C (warm period). The seeds were counted weekly for germination results. A random block, 4

[1] Statistician, Univ. of Nevada, 920 Valley Road, Reno, Nevada 89512.
[2] Range scientist, retired, USDA/ARS, Pasture and Range Management, 920 Valley Road, Reno, Nevada 89512.
[3] Range scientist, USDA/ARS, Pasture and Range Management, 920 Valley Road, Reno, Nevada 89512.

replication, experimental design was utilized with 25 seeds per petri dish (Winer, 1971).

A quadratic response surface was developed for each of the plant species with the general form:

$$Y = A_0 + A_1X_1 + A_2X_2 + A_3X_1^2 + A_4X_2^2 + A_5X_1X_2$$

where

Y = estimated % germination,
A_0 = intercept,
A_1-A_5 = partial regression coefficients for the variables X_1 and X_2,
X_1 = cold temperature, and
X_2 = warm temperature.

The surfaces were generated using standard least squares multiple regression techniques. The partial regression coefficients, A_1-A_5, represent the effect of the specific corresponding independent variable on the dependent variable, Y, with the effects of the remaining independent variables removed. Confidence intervals for each estimated germination value of the temperature regimes tested were derived.

A general linear test approach was used in determining the equality of the response surfaces generated for the six plant species tested (Neter and Wasserman, 1974). Some assumptions needed to be addressed before proceeding with the above method. First, the separate equations had to be of the same general form as previously described, albeit having different intercepts and coefficients. Second, a test for the equality of error variances between the equations had to be performed. This would insure that a transformation of the data, to stabilize variances at an acceptable range, was not needed. Having satisfied the first assumption about equal form for all the equations, we then used a Hartley's F-max test for homogeneity of variance (Ott, 1977). No transformation of our dependent variable, percent germination, was found to be necessary.

Our testing hypotheses were set up as follows. The null hypothesis: no differences exist between the six response surfaces tested, was stated:

H_0: $A_{01} = A_{02} = \ldots = A_{06}$ <u>and</u>

            $A_{11} = A_{12} = \ldots = A_{16}$ <u>and</u>
                    ⋮
            $A_{51} = A_{52} = \ldots = A_{56}$

where

A_{0i} = the intercept of the ith response surface,
$A_{1i}-A_{5i}$= the partial regression coefficients of the ith response surface.
In effect, we are performing a simultaneous comparison of the coefficient vectors of the surfaces for the plant species tested. Our alternative hypothesis: there are differences between some or all of the surfaces tested, was stated:

H_a: any one or more lines stated in H_0 is not true.

The general test of a linear statistical model employs information from full and reduced models in order to formulate a test statistic determining acceptance or rejection of the null hypothesis (Neter and Wasserman, 1974). Assuming that (X_{1j}, X_{2j}, Y_j) = an observation of cold temperature, warm temperature, and percent germination from plant species j, the full model would be:

$$Y_j=A_{0j}+A_{1j}X_{1j}+A_{2j}X_{2j}+A_{3j}X_{1j}^2+A_{4j}X_{2j}^2+A_{5j}X_{1j}X_{2j}+E_j$$

where

A_{0j} = intercept from plant species j,

$A_{1j}-A_{5j}$ = regression coefficients for the corresponding temperature variables, X_{1j} and X_{2j}, for species j

E_j = error term for the jth species.

The full model, called the unrestricted model, provides separate regressions for each plant species. The reduced model, called the restricted model, is the result of the full model being subjected to and modified by the limits imposed by the null hypothesis. The reduced model, in our case, would be:

$$Y_j = A_0+A_1X_{1j}+A_2X_{2j}+A_3X_{1j}^2+A_4X_{2j}^2+A_5X_{1j}X_{2j}+E_j$$

where

A_0 = the common intercept for the 6 plant species combined,

A_1-A_5 = the regression coefficients as common parameters for all 6 plant species combined,

E_j = error term for the pooled 6 plant species.

The reduced model would be a pooling of all 6 plant species data subsequently fitted to one response surface.

The individual error sums of square from the separate regressions, one for each plant species, were added together to get an error sum of squares for the full model. The single regression that was run pooling the observations from the six plant species, provided the error sum of squares for the reduced model. A comparison of these error sums of squares, along with the appropriate degrees of freedom, made up the test statistic. Our test statistic was greater than the corresponding table value, so we rejected the null hypothesis of no differences between the surfaces and concluded that overall differences between the species existed.

Once overall differences between the response surfaces was established, a multiple comparison technique utilizing confidence intervals was performed. These confidence intervals were constructed on the estimated germination means for each of the seedbed temperature areas for each plant species tested. This method of deriving confidence intervals on mean germination at different meaningful locations on the surfaces allows us to find where the differences between the surfaces were occurring.

Average estimated germination was calculated from the response surfaces of each species for distinct categories of seedbed germination temperatures. These seedbed temperature areas were developed on the basis of previous microenvironmental monitoring in the field[4] (Evans et al., 1970; Evans and Young, 1970; Evans and Young, 1972).

RESULTS AND DISCUSSION

Individual Response Surfaces

The quadratic equations derived for the six plant species yielded varied response surfaces of seed germination in relation to temperature. Equations, coefficients of determination, and significant probability levels for the six species were:

crested wheatgrass
$R^2 = 0.66$ (p$\leq$0.01);
$Y = 12.62 + 5.08X_1 + 2.56X_2 - 0.15X_1^2 - 0.06X_2^2 + 0.02X_1X_2$

downy brome
$R^2 = 0.56$ (p$\leq$0.01);
$Y = 28.29 + 5.46X_1 + 2.08X_2 - 0.11X_1^2 - 0.04X_2^2 - 0.06X_1X_2$

Russian thistle
$R^2 = 0.76$ (p$\leq$0.01);
$Y = 59.85 - 1.56X_1 + 3.17X_2 - 0.08X_1^2 - 0.08X_2^2 + 0.06X_1, X_2$

barbwire Russian thistle
$R^2 = 0.60$ (p$\leq$0.01);
$Y = 72.28 - 0.81X_1 + 2.63X_2 - 0.07X_1^2 - 0.09X_2^2 + 0.09X_1X_2$

tumble mustard
$R^2 = 0.72$ (p$\leq$0.01);
$Y = 31.64 + 1.94X_1 + 4.16X_2 - 0.07X_1^2 - 0.07X_2^2 - 0.01X_1X_2$

common mullein
$R^2 = 0.87$ (p$\leq$0.01);
$Y = 2.64 + 2.82X_1 - 2.89X_2 - 0.02X_1^2 + 0.13X_2^2 - 0.06X_1X_2$

Restraints on the above equations were fitted for germination at 0 to 100%. Germination characteristics, due to varied temperature regimes, for each plant species were found by

---

[4] Further refinement in determining seedbed temperature areas is continuing and some preliminary information is being utilized in this paper. Unpublished research, ARS, Reno, NV.

examining the individual response surfaces. Germination was classified by use of distinct seedbed temperature categories (fig. 1). The use of these categories enabled a plant species to be identified as either a cold temperature germinator, a warm temperature germinator, a moderate temperature germinator, a fluctuating temperature germinator, or any combination, depending on which specific seedbed area showed the optimum germination. To determine these optima, the highest estimated germination value for a particular cold/warm temperature combination, minus one half of its confidence interval was compared to the rest of the temperature regimes' estimated germination plus half their confidence intervals. Any overlap between these ranges constituted no statistical difference between these estimated germination values. If these range values failed to overlap, it was concluded that there were significant differences between them.
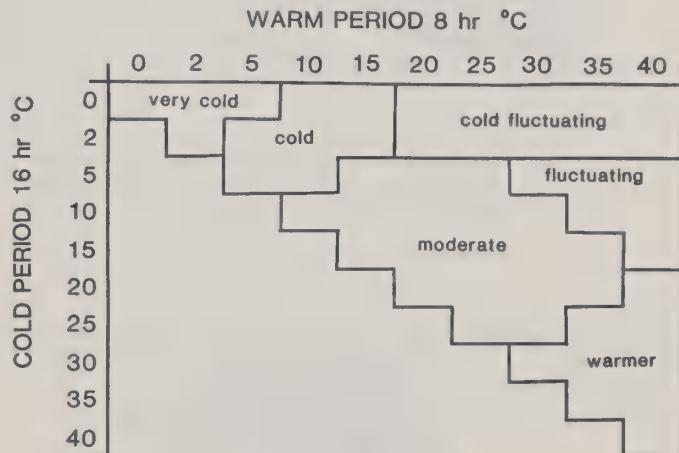
Figure 1. General temperature categories of seed germination based on seedbed monitoring studies.

Crested wheatgrass can be classified as a good moderate temperature germinator with some germination occurring in the warm temperature regimes also. The lowest germination occurred in the very cold temperature ranges (fig. 2). Downy brome had high germination in the moderate seedbed temperature range and lower germination in the very cold and constant warm temperatures (fig. 3). Russian thistle was a high germinator in the very cold, cold, and cold fluctuating ranges with the lowest germination occurring at constant high temperatures (fig. 4). Barbwire Russian thistle had high germination at cold and moderate temperatures and good overall germination elsewhere (fig. 5).
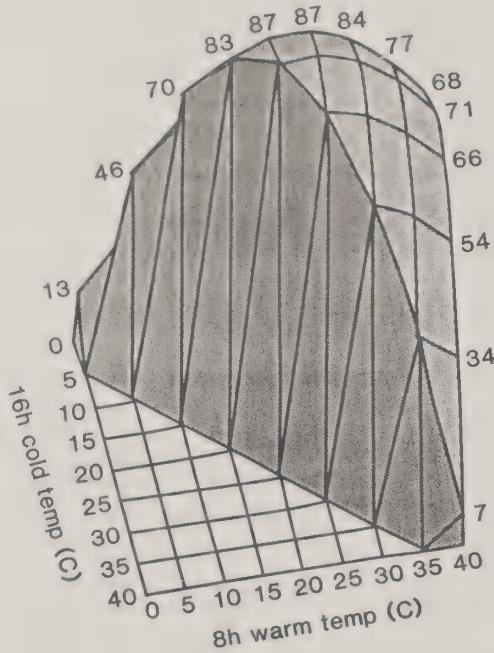
Figure 2.   Quadratic response surface of crested
            wheatgrass germination in relation to
            warm/cold period temperatues.

Figure 4.   Quadratic response surface of Russian
            thistle germination in relation to
            warm and cold period temperatures.

Figure 3.   Quadratic response surface of downy
            brome germination in relation to warm
            and cold period temperatures.
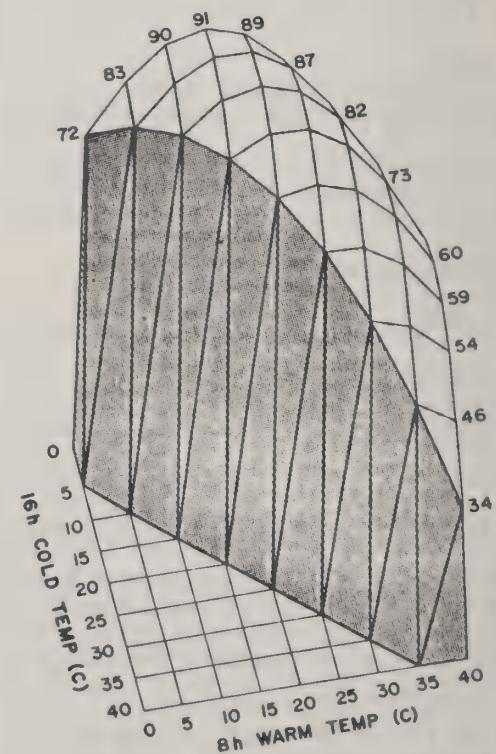
Figure 5.   Quadratic response surface of barbwire
            Russian thistle germination in
            relation to warm and cold period
            temperatures.

Tumble mustard had very high germination
occurring in the moderate and fluctuating
categories, falling off somewhat in the coldest
temperatures (fig. 6). Common mullein had
extremely high germination occuring at the very
warmest end of the fluctuating and warm ranges
and extremely low germination results at the
colder temperatures (fig. 7).

Figure 7. Quadratic response surface of common
mullein germination in relation to
warm and cold period temperatures.

Figure 6. Quadratic response surface of tumble
mustard germination in relation to
warm and cold period temperatures.

Response Surface Comparisons

The general linear test for the equality of the
six surfaces yielded the result, (p≤ 0.01), that
there did indeed exist differences between the
surfaces.

For each of the six species, average estimated
percent germination and corresponding confidence
intervals were calculated at each seedbed
temperature category from the individual response
surfaces. Once germination averages of the
temperature categories were calculated, all

possible cold and warm temperatures that could be
responsible for producing this specific
germination outcome (the average) from the
equation were examined, along with their
corresponding confidence intervals. The widest
(or largest) confidence interval from this group
was selected. We used this very conservative
confidence interval selection method to ensure
that the differences we found were stringent and
undisputable. After calculating and ranking
these mean estimated germinations for each
seedbed temperature area, we compared their
confidence interval ranges (Table 1).

Crested wheatgrass germination closely paralleled
downy brome in its response to temperature, never
once showing any significant differences
(p≤ 0.05) in any of the seedbed temperature
categories tested. Russian thistle, barbwire
Russian thistle, and tumble mustard all had
significantly greater germination (p≤0.05) than
crested wheatgrass in the colder temperature
areas, but no differences in the moderate and
warmer temperatures, although crested wheatgrass
did have higher germination than Russian thistle
in the warm temperature category. Crested

Table 1. Estimated percent germination averages in distinct seedbed temperature categories.

Categories Very Cold Species	Mean	Cold Species	Mean	Cold fluctuating Species	Mean
Barbwire Russian thistle	77 a[1]	Barbwire Russian thistle	87 a	Tumble mustard	91 a
Russian thistle	66 a	Russian thistle	79 ab	Russian thistle	78 ab
Tumble mustard	42 b	Tumble mustard	69 bc	Barbwire Russian thistle	67 bc
Downy brome	35 bc	Downy brome	55 cd	Downy brome	55 cd
Crested wheatgrass	20 c	Crested wheatgrass	42 d	Common mullein	44 d
Common mullein	2 d	Common mullein	1 e	Crested wheatgrass	35 d
Fluctuating		Moderate		Warm	
Tumble mustard	95 a	Tumble mustard	94 a	Common mullein	78 a
Common mullein	80 b	Barbwire Russian thistle	83 ab	Tumble mustard	69 a
Downy brome	66 bc	Downy brome	82 ab	Barbwire Russian thistle	55 ab
Russian thistle	65 bc	Crested wheatgrass	78 ab	Crested wheatgrass	53 ab
Barbwire Russian thistle	61 c	Russian thistle	65 b	Downy brome	41 b
Crested wheatgrass	56 c	Common mullein	29 c	Russian thistle	16 c

[1]   Means followed by the same letters are not significantly different ($p \le 0.05$) based on overlap of the confidence intervals.

wheatgrass had significantly greater germination ($p < 0.05$) than common mullein in the very cold and cold temperature ranges, but when warm temperatures became higher, there were no differences between them, even though common mullein had the highest germination of any species in these ranges.

Like crested wheatgrass, downy brome had lower germination in the colder temperatures than either Russian thistle or barbwire Russian thistle, also having higher germination than Russian thistle in the warm temperature area. Unlike crested wheatgrass, downy brome showed comparable germination to tumble mustard in the colder temperatures, but had less germination in the fluctuating and warm areas. Downy brome had higher germination than common mullein at colder and moderate temperatures, but significantly less germination ($p \le 0.05$) at the warmer temperatures.

Russian thistle and barbwire Russian thistle had the same germination responses in all of the temperature categories except in the warm area, where barbwire Russian thistle showed significantly greater germination ($p < 0.05$). In the moderate, fluctuating, and warm temperature ranges, tumble mustard had greater germination than did Russian thistle. There were no differences between these two species at cold and cold fluctuating temperatures, and Russian thistle showed greater germination than tumble mustard at the coldest temperatures. Russian thistle had consistently higher germination than common mullein in all of the temperature categories except warm, where common mullein showed superior germination, and fluctuating, where there were no differences.

Barbwire Russian thistle had significantly greater germination ($p \le 0.05$) than tumble mustard in the colder temperature ranges but, unlike Russian thistle, showed no differences in the moderate and warm categories. When fluctuating temperatures were tested, tumble mustard showed greater germination than barbwire Russian thistle. Barbwire Russian thistle's germination results, like most of the other species tested, were higher than those of common mullein in the cold temperature areas, and had the same results as crested wheatgrass to common mullein in the warm temperatures.

Tumble mustard showed greater germination than common mullein in all temperature categories except warm, where common mullein, again, had the higher germination response.

Comparisons of these six plant species, based on biologically distinct sections of their response surfaces, help in determining what types of seedbed environments are best suited for each species, and which particular species is best suited for a particular seedbed environment.

Based on the above comparisons, Russian thistle and barbwire Russian thistle had the best germination results in the colder temperature areas and also did well in the moderate temperature zone. Crested wheatgrass and downy brome had the highest germination in the fluctuating and moderate temperature areas. Tumble mustard did fairly well at cooler temperatures, but showed highest germination in the fluctuating and moderate temperature ranges. Common mullein was the most unique of

any of the six species tested, and can be classified as a warm temperature germinator.

SUMMARY AND CONCLUSIONS

Multiple comparisons, such as the use of Duncan's Multiple Range Test, are inappropriate analytical tools when comparing between levels of a quantitative factor. Multiple regression and confidence interval techniques are statistically suited to solving these types of analyses.

Individual response surfaces and their confidence intervals, estimating germination from cold and warm temperature regimes, provide valuable information on how temperature affects the germination of a particular plant species. The adaptability of a plant species to a specific temperature environment can then be assessed. Biologically distinct seedbed temperature areas can be used to categorize a plant species as either a cold, fluctuating, moderate or warm temperature germinator.

For a specific seedbed temperature environment that starts out cold, warms up slowly to fluctuating and moderate temperatures but never gets too warm, both barbwire Russian thistle and Russian thistle would be highly adaptive. Tumble mustard germinates in fluctuating, moderate and warmer temperatures, so it would be suited to this type of environment when the colder temperatures started to warm up. Common mullein needs warm temperatures in order for germination to occur, which would make this species a poor candidate for this environment. Crested wheatgrass and downy brome germinate best at moderate temperatures and would not seem to do well either.

Comparisons between response surfaces provide even more information on the seedbed temperature requirement similarities of differerent plant species. Confidence interval comparisons of these temperature categories between different plant species aids in determining which species is most suitable to a particular environment.

Using the temperature environment specified above, barbwire Russian thistle and Russian thistle would be the most suited to germinating and establishment followed by tumble mustard as the temperatures became warmer. Downy brome, crested wheatgrass and common mullein would be the least suited to this particular environment.

LITERATURE CITED

Chew, Victor. 1976. Comparing treatment means: A compendium. Hort Science 11:348-357.

Evans, Raymond A., Richard Holbo, Richard E. Eckert, Jr., and James A. Young. 1970. Functional environment of downy brome communities in relation to weed control and revegetation. Weed Science 18:154-162.

Evans, Raymond A. and James A. Young. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. Weed Science 18:697-703.

Evans, Raymond A. and James A. Young. 1972. Microsite requirements for estabishment of annual rangeland weeds. Weed Science 20:350-356.

Evans, Raymond A. and James A. Young. 1982. Microhabitat variation in relation to weed seed germination and seedling emergence. In: Biometeorology in Integrated Pest Management. Academic Press, Inc.

Evans, Raymond A., Debra A. Easi, Don N. Book, and James A. Young. 1982. Quadratic response surface analysis of seed-germination trials. Weed Science 30:411-416.

Neter, John and William Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, IL. 842 p.

Ott, Lyman. 1977. An introduction to statistical methods and data analysis. Duxbury Press. North Scituate, MA. 730 p.

Peterson, R.G. 1977. Use and misuse of multiple comparison procedures. Agron. J. 69:205-208.

Semenza, R.J., J.A. Young, and R.A. Evans. 1978. Influence of light and temperature on the germination and seedbed ecology of common mullein (Verbascum thapsus). Weed Science 26:577-581.

Winer, B.J. 1971. Statistical principles in experimental design. Second Edition. McGraw-Hill, Inc. 907 p.

Young, James A. and Raymond A. Evans. 1979. Barbwire Russian thistle seed germination. Journal of Range Manage. 32:390-394.

Young, James A. and Raymond A. Evans. 1982. Temperature profiles for germination of cool season range grasses. U.S. Dept. of Agric., Agric. Res. Serv., Agric. Res. Results. ARR-W-27. 91 p.

EARLY ROOT LENGTH DISTRIBUTIONS OF WARM SEASON
PERENNIAL GRASSES AS INFLUENCED BY SOIL MOISTURE:
A MODELING CONCEPT

Gary W. Frasier and J. Roger Simanton[1]

ABSTRACT

Soil moisture availability is one of the most
important factors controlling root elongation
during seedling establishment. A procedure is
presented for combining information of the rate of
early root elongation with soil moisture
distribution drying data to evaluate the chances
of successful seedling establishment.

INTRODUCTION

"A knowledge of root relations leads to the
intelligent solution of problems of range
management and improvement and, indeed, to all
problems where natural vegetation is concerned"
(Weaver and Clements 1929, p. 216).

"It is probably impossible to think of an aspect
of plant physiology which reveals greater
ignorance and confusion than that which is
concerned with natural regulation of growth and
differentiation in roots." (Wareing and Phillips
1978, p. 114).

Without adequate root growth, the chances for a
plant's success are greatly reduced. Roots absorb
water and nutrients from the soil for transport to
the plant stem; they are the site of synthesis of
some plant hormones; they may act as food storage
organs; and they anchor the plant to the soil
(Russell 1973). One of the most critical phases
of a plant's life is in the germination to early
seedling stage when the plant's survival is
dependent upon the moisture uptake of the seminal
root (Mueller and Weaver 1942, Tapia and Schmutz
1971). During this period, the root system must
be most efficient in supplying the developing
seedling with moisture. Root elongation rates must
be sufficiently high to maintain contact with the
receding soil moisture front if the seedling is to
survive.

This paper presents a conceptual model of the
approach for combining root elongation data with
soil moisture distribution data during drying for
evaluating seedling survival characteristics.
Data used in the paper are derived from various
studies which were not designed to evaluate our
hypothesis. As such, the results are meant to be
used only to illustrate points and not to construe
real differences that might be expected in
laboratory or field situations.

BACKGROUND

Little information is available on the early
rooting characteristics of range grasses. The
majority of the literature refers to root growth
studies of older-aged agronomic species with
specific reference to field established plants.

Limited studies have indicated differences in root
elongation rates among species. Wilson and Briske
(1979) found that seminal root elongation rates of
blue grama (Bouteloua gracilis (H.B.K. Lag. ex.
Griffiths) ranged from 6 to 10 mm per day. A
quadratic equation was used to fit root length
(cm) versus time (days). Sosebee and Herbel
(1969) reported that 21 days after planting,
sideoats grama (Bouteloua curtipendula (Michx.)
Torr.) had an average length of 96 mm and that
alkali sacaton (Sporobolus airoides Torr.) had an
average length of 38 mm. Simanton and Jordan
(1986) mean root lengths at 165 hours of 16 mm for
Cochise lovegrass (Eragrostis lehmanniania Nees X
E. trichophora Coss and Dur.) to 67 mm for
sideoats grama. These differences in root
elongation rates are not considered either fast or
slow. Since these plants have been successfully
established in various semiarid regions it would
be concluded that the roots can keep up with a
soil drying front, at least with some
soil-climatic conditions. We also know that there
have been unsuccessful seedings.

Soil moisture stress is probably the most common
and thus important root growth limiting condition.
Root elongation responses to soil moisture stress
varies not only in magnitude among species but
also in the critical moisture stress which
significantly affects root growth. Native grass
species, Bouteloua gracilis and Agropyron smithii,
showed a root elongation cessation at soil water
potential of -16.6 bars and -8 bars, respectively
(Majerus 1975).

Soil moisture is seldom uniformly distributed
throughout the soil profile and root growth may be
restricted in an area of low soil moisture. This
may be compensated for by greater growth in an
area favorable in soil moisture (Russell 1973).
Root growth studies have indicated that roots will
normally only grow into moist soil zones
(Hendrickson and Veihmeyer 1931, Trouse 1972).
There is evidence though that some warm season
grass species will grow into soil zones where the
moisture level is below the wilting point (Salin,
et al. 1965). Roots have been observed to
elongate into dry soil (-40 bars) as long as the
plant water potential remained sufficiently high
and that water was available to other parts of the
root system (Portas and Taylor 1976).

MODEL CONCEPT

It is hypothesized that the rate of primary root
elongation can be combined with soil moisture data
or models of soil moisture distribution during
drying to estimate probabilities of seedling
survival and plant establishment. This would
allow the use of rainfall probability data to
estimate the optimum time for seeding or to select
the optimum species for seeding under a specific
rainfall, soil-moisture regime.

[1] Research Hydraulic Engineer and Hydrologist,
respectively; USDA-ARS, Aridland Watershed
Management Research Unit, 2000 East Allen Road,
Tucson, Arizona 85719.

Mathematical models have been developed to describe soil water movement, with reference to plant roots; in both saturated and unsaturated soils (e.g., Belmans, et al. 1979, Gardner 1964, Hillel, et al. 1976, and Qashu et al. 1973). Experimental analyses suggest that both the root and soil resistances play an important role in movement of water to roots. Belmans, et al. (1979) found that soil resistance to root penetration may dominate through the lower range of plant available soil moisture levels and that soil hydraulic resistance becomes more important as the soil moisture becomes depleted. Soil water potential in the surface 10 cm of semiarid soils is not maintained above -15 bars for extended periods in the summer (Noy-Meir 1973). Over a period of time, possibly only a few days, roots need to elongate into moist soil to keep soil water resistances from getting so large that the plant cannot extract enough water to grow or survive. Models of soil surface moisture evaporation have been proposed that can give estimates of temporal and spatial moisture amounts during the seed to seedling stages of a plants life (Ritchie et al. 1976). These models stress the importance of root elongation into the soil and, if coupled with time-dependent root elongation relationships, could be useful in estimating success in establishment of range grass seedlings.

This root elongation, soil moisture model assumes that a seed has germinated under field capacity conditions and if the germinated seed is to emerge and become a established plant, the primary root elongation rate must exceed the rate of the receding soil moisture front (fig. 1). Without additional water, the germinated seeds and seedling of species with root elongation rates less than the rate that the soil moisture front recedes into the soil will die. Distributions of root elongation rates needed for such a model could be experimentally determined for selected plant species grown under various moisture, temperature, and soil conditions. Also, test environments could be designed to meet comparable natural conditions.

Soil moisture distributions over time for different texture classes could either be experimentally determined or estimated using current or developed soil moisture evaporation models (fig. 2). These models can be as simple or as complex as needed to relate soil water loss in the seeding zone to various soil and climatic factors.
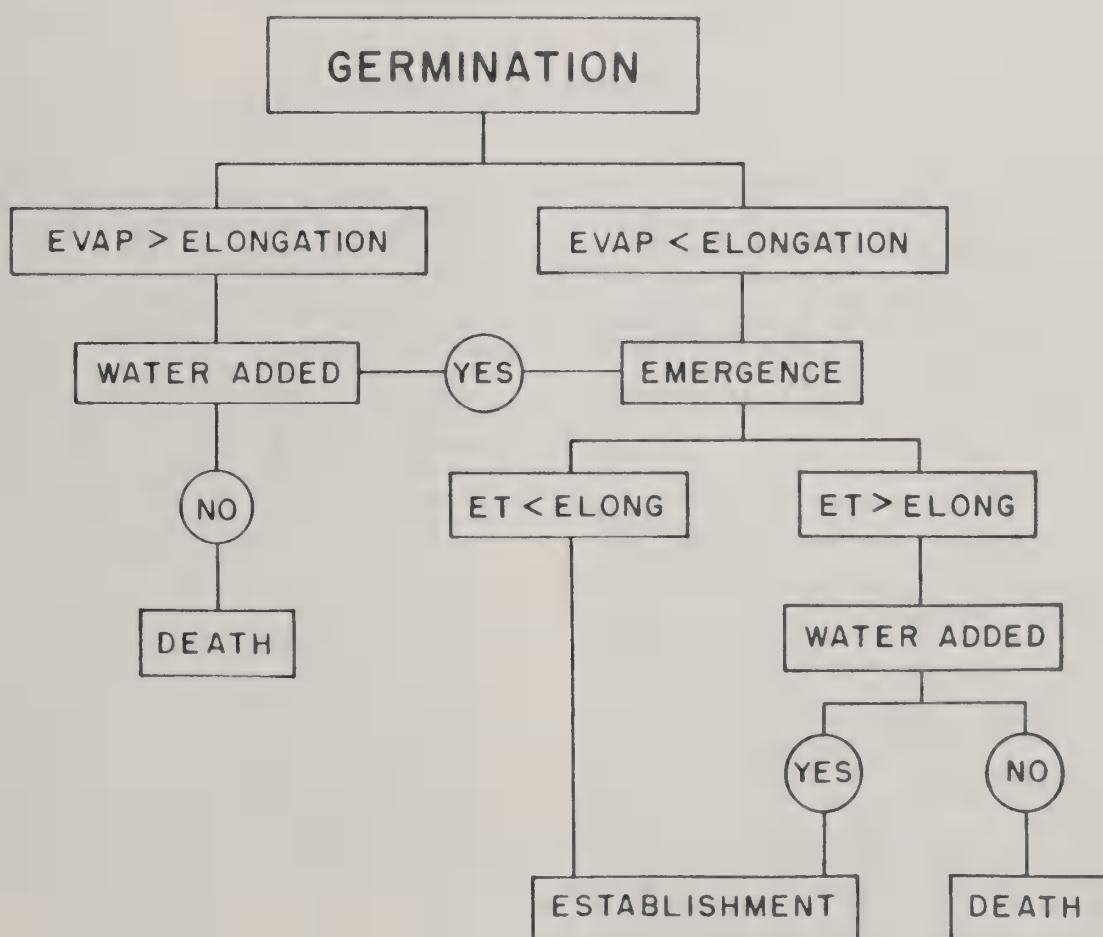
Figure 1.   Model concept of root elongation versus
soil water loss by evaporation.
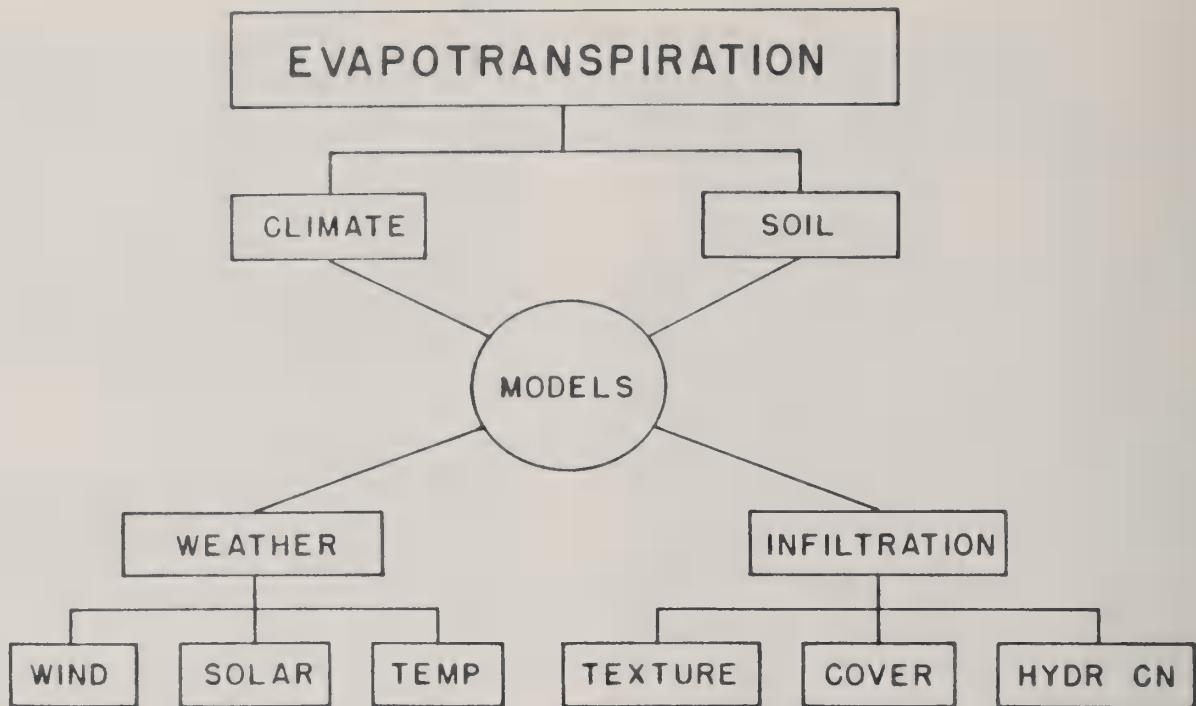
Figure 2. Conceptual evapotranspiration model.

Irrespective of the source of the soil water, precipitation or runon, the various parameters associated with water availability can be assigned probabilities of likely occurrence (fig. 3). It is then possible to develop a complete description of soil water availability for various rangeland regions. Root length distribution probabilities coupled with the soil moisture and rainfall probabilities could give probabilistic estimates of seeding successes.

MATERIAL AND METHODS

The root elongation data for the paper was obtained from studies conducted at the USDA-ARS, Aridland Watershed Management Research Unit, Tucson, Arizona. Portions of the data were reported by Simanton and Jordan (1986). The soil moisture drying data was obtained from Ray Jackson, USDA-ARS, U.S. Water Conservation Laboratory, Phoenix, Arizona. Portions of the data have been reported by others.

Root Elongation Studies

Root lengths of 5 warm season range grasses were determined at 12 hr intervals from seed germination to early seedling stage of 5 days. Grass species used were "Premier' sideoats grama, Cochise lovegrass, 'A-130' blue panicgrass (Panicum antidotale Retz.), and accessions "PMT-1733-77" and "NM-184" alkali sacaton.

Seedlings were grown in cylinders made from 150-mm lengths of 25-mm diameter polyvinylchloride pipe cut in half lengthwise. The 2 halves were held together with rubber bands to form a cylinder open at both ends. The cylinders were placed upright in a holding tray and filled with 135 g of 20 mesh white silica sand. One seed was placed on the surface of each half of each cylinder and covered with 5-mm of sand. The sand was watered to field capacity with 15 ml of distilled water. The study was conducted in a light and temperature controlled growth chamber with alternating temperatures of 30 and 22°C and relative humidity near 100%. There were 14 hr of light and high temperature alternated with 10 hr of darkness and low temperatures. These sequences were similar to those reported as optimum for germination and seedling growth of the species studied (Knipe 1967, Sosebee and Herbel 1969).

Root length measurements were begun 12 hrs after germination was first observed in an adjacent seed germination study and then each succeeding 12 hrs. At each evaluation time, 10 cylinders for each species were randomly selected, separated and the root length measured to the nearest millimeter. The total number of roots at each millimeter length increment were tabulated for root-length distribution analysis for each evaluation period.
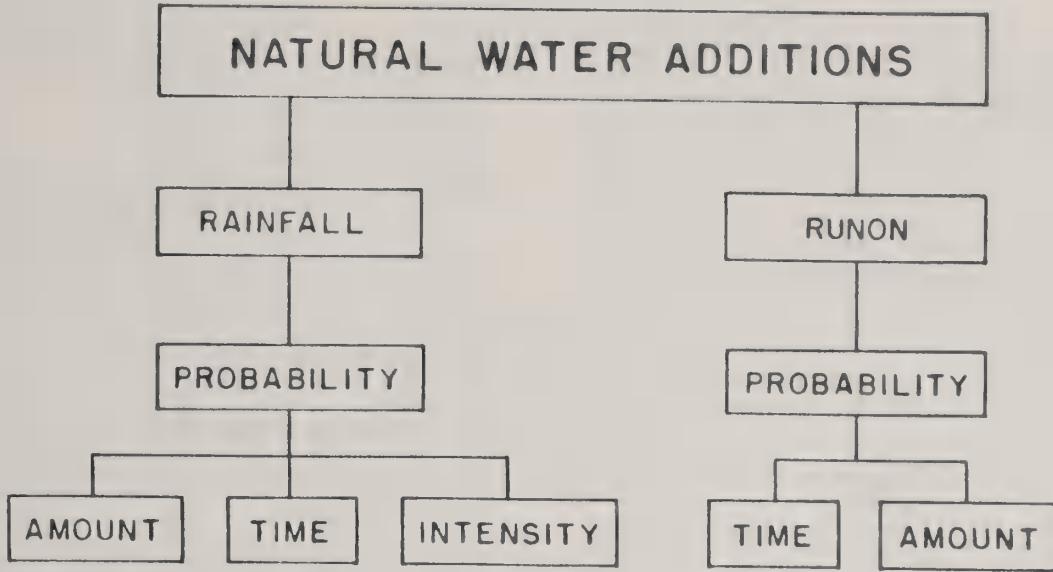
Figure 3. Conceptual water application effects to root elongation model.

Soil Water Characteristics

The experimental site was a 72 by 90-m field at the U.S. Water Conservation Laboratory, Phoenix, Arizona. The soil was a reasonably uniform loam texture to a depth of about 100 cm. The area was leveled and watered by flood irrigation between borders. Following irrigation, soil water contents were measured gravimetrically. Soil samples were taken of the 0- to 0.5-cm depth and in 1-cm increments to 5 cm depth and in 2-cm increments from 5 to 10 cm depth. Samples were taken at 0.5-hr intervals from 4 March to 19 March. Six sites were sampled at each time and composited for each depth increment. Water contents were converted to volumetric basis by multiplying by the bulk density (Jackson, 1973). The soil water contents were converted to soil moisture tensions by the equation:[1]

$$\psi = \exp\,[14.86 + 25.65\theta - 1773.7\theta^2 + 19163.2\theta^3 - 97687.7\theta^4 + 236565\theta^5 - 218317\theta^6$$

where ψ = soil moisture tension in bars, and θ = volumetric water content.

RESULTS AND DISCUSSION

The root elongation study was conducted on a silica sand maintained at approximately field capacity (<-0.3 bars) for the duration of the study period. Because of this, we don't know how the root elongation rate at various soil moisture tensions compares to that measured at zero water stress. It is known that soil moisture tension in the seedbed layer is at field capacity for only a very short time, in the order of a few hours. For purposes of the paper we have arbitrarily selected the range of 0 to -2 bars to represent zero water stress. Therefore, soil water tensions greater than -2 bars represent a condition at which the root would no longer elongate. Because of the conceptual nature of the model and limited data to analyze, we are not considering the interactions that might occur between temperature and water nor the effects soil texture might have on root elongation rate. Also, only the data from the sideoats grama and Cochise lovegrass is used in the discussions.

Jackson (1973) reported on the phenomena of soil moisture redistribution or rewetting of the soil surface layers during the evening and nighttime periods. These changes in soil water contents between the times of 0600 and 1800 hours represented fluctuations in soil moisture tensions of 1 to 2 orders of magnitude with the driest period occurring in late afternoon. For our discussion, we selected the soil moisture values measured at 1800 in the evening and have not addressed the effect of root elongation during cyclic water contents such as what happens during moisture redistribution. All times were referenced to 1800 on 5 March when the surface 2-cm had drained to water contents representing -0.3 bars (irrigation applied on the afternoon of 2 March).

---

[1] Personal communication, R.D. Jackson, U.S. Water Conservation Laboratory, Phoenix, Arizona.

The distribution of soil moisture tensions with depth for 24 and 144 hr for the Phoenix data are presented on the left side of figure 4. The root distribution of sideoats grama for two evaluation periods, 34 and 140 hrs after seed germination are presented on the right side of figure 4. At both time periods, root lengths for the majority of the samples were greater than the depth to the -2 bar soil moisture tension. This implies that the root elongation rate was faster than the soil drying rate and that the seedling would not have encountered water stresses that would have affected growth.
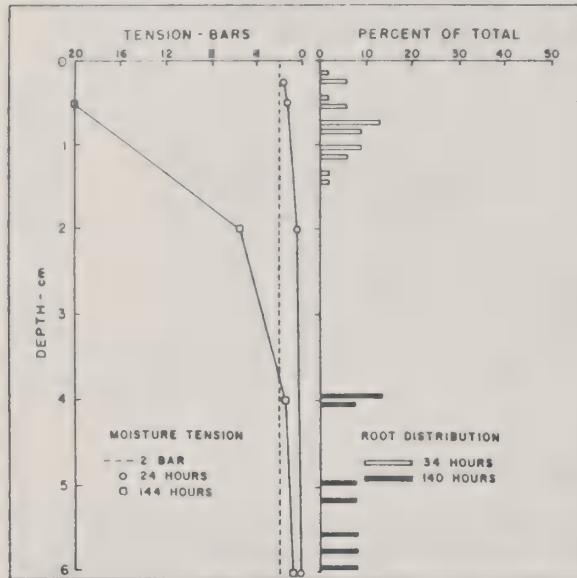
Figure 4. Soil drying and root distribution for sideoats grama.

Similar data are presented in figure 5 for Cochise lovegrass. Root elongation rates were slower than the soil moisture drying front which, if some other adjustment (physiological) wasn't made by the plant or if the soil didn't receive a water addition, the seedling would die.

SUMMARY

The rate of root elongation is critical to seedling establishment. As the soil dries downward from the surface, the root must be able to maintain contact with moist soil or the seedling will die. A simple model was developed that combined root elongation rate to soil moisture availability during drying. There is little information on the rooting characteristics of range grasses. Root elongation data from a simple laboratory study was combined with soil moisture tension drying data derived from a bare soil area following irrigation. It was shown that with root elongation faster than the rate of soil drying there was a good probability that the seedling would survive. If the soil moisture drying front moved into the soil at a faster rate than the root elongated, the seedling would be expected to die. This approach can be used to assist in estimating, based upon soil, climate, and species rooting properties, the chances of achieving successful seedling establishment.
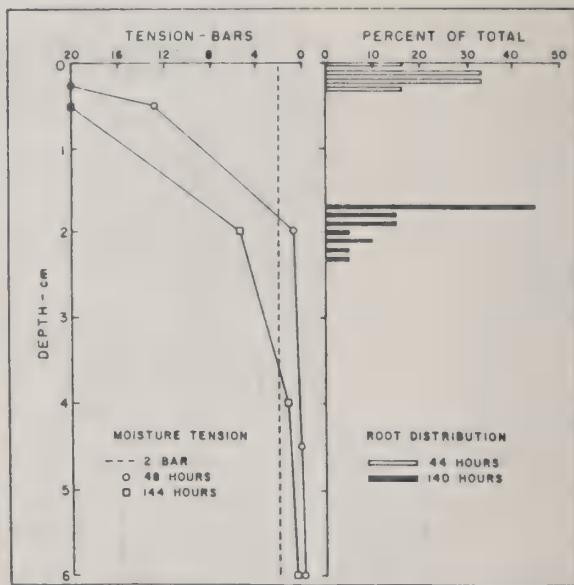
Figure 5. Soil drying and root distribution for Cochise lovegrass.

LITERATURE CITED

Belmans, C., J. Feyen, and D. Hillel. 1979. An attempt at experimental validation of macroscopic-scale models of soil moisture extraction by roots. Soil Sci. 127:174-186.

Gardner, W. R. 1964. Relation of root distribution to water uptake and availability. Agron. J. 56(1):41-45.

Hendrickson, A. H. and F. J. Veihmeyer. 1931. Influence of dry soil on root extension. Plant Phys. 6:567-576.

Hillel, D., H. Talpaz, and H. van Keulen. 1976. A macroscopic-scale model of water uptake by a nonuniform root system and of water and salt movement in the soil profile. Soil Sci. 121:242-255.

Jackson, R.D. 1973. Diurnal changes in soil water content during drying. In. Field Soil Water Regime. Soil Sci. Soc. Amer., Madison, WI.

Knipe, O.D. 1967. Influence of temperature on the germination of some range grasses. J. Range Manage. 20:278-299.

Majerus, M. E. 1975. Response of root and shoot growth of three grass species to decreases in soil water potential. J. of Range Mgt. 28(6):473-476.

Muller, I.M., and J.E. Weaver 1942. Relative drought resistance of seedlings of dominant prairie grasses. Ecology 23:387-398.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Sys. 4:25-51

Portas, C. A. M. and H. M. Taylor. 1976. Growth
and survival of young plant roots in dry soil.
Soil Sci. 121(3):170-175.

Qashu, H. K., D. D. Evans, M. L. Wheeler, and T.
Sammis. 1973. Water uptake by plants under
desert conditions. USIBP Research Memorandum
RM73-42. University of Arizona.

Ritche, J.T., E.D. Rhodes, and C.W. Richardson.
1976. Calculating evaporation from native
grassland watersheds. Trans. ASAE 19:1098-1103.

Russell, E. W. 1973. Soil Conditions and Plant
Growth. Longman Group Lmt. London. 849 p.

Salin, M. H., G. W. Todd, and A. M. Schlehuber.
1965. Root development of wheat, oats, and barley
under conditions of soil moisture stress. Agron.
J. 57(6):603-607.

Simanton, J.R. and G.L. Jordan. 1986. Early root
and shoot elongation of selected warm-season
perennial grasses. J. Range Manage. 39:63-67

Sosebee, R.E. and C.H. Herbel. 1969. Effects of
high temperature on emergence and initial growth
of range plants. Agron. J. 61:621-624.

Tapia, C.R. and E.M. Schmutz. 1971. Germination
responses of three desert grasses to moisture and
light. J. Range Manage. 24:292-295.

Trouse, A., Jr. 1972. Effects of soil moisture
in plant activities. p. 246-247. In: W. M.
Carleton (ed.): Compaction of agricultural lands.
Am. Soc. Agr. Eng. St. Joseph, Michigan.

Wareing, P. F. and I. D. J. Phillips. 1978. The
Control of Growth and Differentiation in Plants.
Pergamon Press. Oxford.

Weaver, J. E. and F. E. Clements. 1929. Plant
Ecology. McGraw-Hill. New York. 520 p.

Wilson, A.M. and D.D. Briske. 1979. Seminal and
adventitious root growth of blue grama seedlings
on the Central Plains. J. Range Manage. 32:209-213

THE SIMULATION OF PLANT BIOGRAPHY

Jon D. Hanson and Richard L. Olson, Jr.[1]

ABSTRACT

ARS has recently developed several systems-level
models, including a general grasslands model
(SPUR Phase I). Phase II development of SPUR,
already under way, will include a model of early
plant biography, from seed-dormancy through
seedling establishment. Past plant development
models include those dependent solely upon
temperature (degree-day and biophysical),
statistical, decision-tree and matrix
formulations. Our model fits into the latter
category, being based on an Usher matrix. The
model consists of four explicit life stages
(dormant seeds, germinated seeds, emerged seeds,
established seedlings) and an implicit stage
(death). The probabilities of graduating from
one stage i to another stage j in a time interval
Δt are proportional to environmental parameters.
The formulation will bring added power to the
SPUR model, and be useful as a stand-alone model
as well.

INTRODUCTION

National legislation, during the last several
years, has induced the Agricultural Research
Service (ARS) to develop several systems level
models. Clean water legislation led to the
development of ACTMO (Agricultural Chemical
Transport Model) in 1975, and subsequently CREAMS
(Chemicals, Runoff, and Erosion from Agricultural
Management Systems) in 1979 (Knisel 1980). In
1984, EPIC (Erosion/Productivity Impact Calcula-
tor) was completed (Williams et al. 1983) in
response to the 1977 Soil and Water Conservation
Act. In 1985, ARS began work on WEPP (Water
Erosion Prediction Project) in an effort to
respond to several conservation laws.

The above mentioned efforts focused purely on
cropping systems, and the problems encountered in
developing models for rangeland were ignored. In
1978, a range modeling workshop was held to begin
planning the development of a general grassland
model; the model was officially started in 1981
and given the name SPUR (Simulation of Production
and Utilization of Rangelands) (Wight 1983).
SPUR Phase I has been completed and final docu-
mentation is in press. Planning for SPUR Phase
II was initiated in 1985. Restructuring of the
personnel to complete the SPUR Phase II effort
was completed in late 1985.

The SPUR Phase I model is a general grassland
simulation model composed of five basic
components: hydrology, plant growth, animals
(domestic and wildlife), and economics. The
model is driven by daily inputs of precipitation,
maximum and minimum temperatures, solar radia-

tion, and wind run. These variables are derived
either from existing weather records or from use
of a stochastic weather generator. The hydrology
component calculates upland surface runoff
volumes, peakflow, snowmelt, upland sediment
yield, and channel streamflow and sediment yield
(Springer et al. 1984). Soil water tensions,
used to control various aspects of plant growth,
are generated using a soil-water balance equation
(Lane 1985). Surface runoff is estimated by the
Soil Conservation Service curve number procedure,
and soil loss is computed by the Modified
Universal Soil Loss Equation (Williams 1975).
The snowmelt routine employs an empirical
relationship between air temperature and energy
flux of a dynamic snowpack.

In the plant component, carbon and nitrogen are
cycled through several compartments including
standing green, standing dead, live roots, dead
roots, seeds, litter, and soil organic matter
(Skiles et al. 1983, Hanson et al. 1985a, Hanson
et al. 1985b). Inorganic soil nitrogen is also
simulated. The model simulates competition for
water and nitrogen between plant species and the
impact of grazing on vegetation. Required
initial conditions include the biomass content
for each compartment and parameters that charac-
terize the species to be simulated.

The calculation of domestic livestock physiology
and forage harvesting by wildlife is accomplished
in the animal component (Rice et al. 1983).
Detailed growth information is provided for
cattle on a steer-equivalent basis using an
adaptation of the Texas A&M Beef Model (Sanders
and Cartwright 1979). Forage consumption is
calculated for all animal classes based on forage
palatability, abundance, and location. The
development of preference vectors to control
plant utilization by animals is a unique feature
of the model. Wildlife species including insects
are considered to be fixed consumers and are
given first access to the available forage.
Animal production and net gain are used by the
economic component to estimate benefits and costs
of alternative grazing practices, range improve-
ments, and animal management options.

Two versions of SPUR have been developed. The
first version simulates a grazing unit or field.
This version allows grazing animals to graze
different parts of the unit according to various
location preference vectors. Plant dynamics and
the impact of grazing on rangeland are simulated
in the field-scale version. The field-scale
version is capable of simultaneously simulating a
maximum of seven plant species growing on as many
as nine sites with no restrictions on size of the
sites.

The second version of SPUR simulates a basin or
watershed and requires considerable averaging of
animal and plant attributes. This version,
however gives high resolution for runoff,
peakflow, sediment yield, and channel hydrology.
It predicts runoff and sediment yield for basins
of up to 26 km^2 containing up to 27 hydrologic
units.

As currently implemented, the SPUR model does not simulate annual plants, thus excluding many important rangeland plant species from analysis. A major thrust of the SPUR Phase II plant modeling effort will be the development and inclusion of a rangeland plant colonization module. Numbers of dormant seeds, germinated seeds, emerged plants, and established plants will be simulated for each species. The purpose of this paper is to describe the types of models already constructed for simulating plant biography and to systematically analyze the plant colonization problem, thereby developing a framework by which a new model can be created.

PLANT COLONIZATION MODELS

A complete model of plant colonization within natural or agronomic communities must include descriptions of seed production, dissemination, germination, emergence, and establishment. Unfortunately, these processes are generally modeled separately and usually deal with only a single-plant species (Pacala and Silander 1985). A complete discussion of plant-population dynamics can be found in Harper (1977). Existing formulations that discuss plant biographgy components can be classified into four general categories or approaches.

Temperature Dependent Models

These models are controlled only by temperature and are used to predict germination rates, emergence, and other aspects of plant development. The most widely used model of this type utilizes the "degree-day" concept. Degrees are accumulated by summing the deviation of the average daily temperature from some lower threshold temperature. Then, by knowing the number of degree days needed for completion of a process, a prediction of its progress can be made. Wilson and Barnett (1983) defend this procedure and give examples of its utility.

Another type of temperature dependent model was presented by Goloff and Bazzaz (1975). Their paradigm assumes that plant development coincides with an Arrhenius type system, based on monomolecular reaction kinetics. In simplest form, this type of emulation assumes that development rate is inversely proportional to temperature. Sharpe and DeMichele (1977) have generalized this formulation and shown its utility for many poikilotherms.

Statistical Models

Models of this type use field data to predict crop yields (which can be all or part of the above- and belowground plant biomass.) Thornley (1983) discussed a single-equation that related planting density to crop yield. Optimum plant density for maximum corn yield was predicted by Carmer and Jackobs (1965) and the effect of plant competition and and row spacing on the yield of root crops was empirically estimated by Benjamin

(1982). Statistical distributions have also been used to describe the processes involved in plant colonization, particularly seed germination rates. Distributions used include the gamma distribution (Thornley 1977), the logistic growth function (Schimpf et al. 1977, Hsu et al. 1984, and Waggoner and Parlange 1974), and the von Bartalanffy's growth function (Richards 1959). Though these technique are generally very useful in describing a particular data set, they cannot be adapted easily to other plant species or locations.

Decision Tree Models

These formulations do not implicitly state a growth equation or statistical distribution. Rather, a decision tree is developed. Bould and Abrol (1981) assumed each seed in a population at the various nodes of the tree had the same probability of germinating in unit time. Frasier (1986) determined the probability of moving along a particular pathway based on specific environmental conditions, namely soil moisture and temperature.

Matrix Models.

Matrix methods fall into two general classes: stochastic and deterministic. Stochastic methods most-often used are Markov processes, based on the work of the Russian mathematician A.A. Markov in the early 1900's. They can be subdivided into two categories: discrete-time and continuous-time processes. Discrete-time processes (i.e., the time-steps are equal) have been used successfully in a variety of biological applications, most notably to model successional phenomena (Anderson 1966, Williams et al. 1969, Horn 1975). Continuous-time processes (i.e., the time intervals can be of varying lengths) have been used to model plant physiology (Olson et al. 1985, Sharpe et al. 1985, Wu et al. 1985). Markov mathematics assumes that the system under investigation can exist in two or more states, S_1 through S_n, where n equals the number of possible states. The state variables in a Markov process are the steady-state probabilities Π_i that the system is in State (i) at any time (t). Steady-state formulations, however, do not work well when the time spent in any one state is large compared to the time between changes in model parameter values.

Of the deterministic matrix methods, the most popular in ecological modeling have been the Leslie matrix and its modifications. The Leslie matrix (Leslie 1945) assumes a population life-history can be divided into (n) discrete age classes, each having associated with it an age-specific fecundity rate (f). In addition, each class (j) has a probability p_{ij} of surviving to the next age class (i) (note that these probabilities are similar to the single-step probabilities in a Markov chain). Leslie arranged these values into a matrix L:

$$\begin{pmatrix} f_0 & f_1 & f_2 & \cdots \\ p_{10} & 0 & 0 & \cdots \\ 0 & p_{21} & 0 & \cdots \\ 0 & 0 & p_{32} & \cdots \\ \vdots & \vdots & \vdots & \end{pmatrix}$$

where f_j is the fecundity of age class j, j = 0, ..., n-1. To arrive at the number in each class at any time t+1, L is multiplied by $N(t)$, the column vector of $n_j(t)$, the number of organisms in class j at time t:

$$N(t+1) = L \cdot N(t).$$

MODEL DEVELOPMENT

The technique used for our model is similar to the Usher modification of the Leslie matrix (Usher 1966). In the Leslie matrix, the time-step Δt is equal to the age-class length. In other words, at the end of each time-step (class), the organism either dies or progresses to the next age class. The Usher matrix allows for varying time-steps by including, in addition to the probabilities p_{ij} of going from one step to the next, the probability of staying in each age class an additional time step, p_{ii}. These probabilities are added to the diagonals of L, producing the "Usher matrix", U:

$$\begin{pmatrix} (f_0 + p_{00}) & f_1 & f_2 & \cdots \\ p_{10} & p_{11} & 0 & \cdots \\ 0 & p_{21} & p_{22} & \cdots \\ 0 & 0 & p_{32} & \cdots \\ \vdots & \vdots & \vdots & \end{pmatrix}.$$

We assume four explicit stages in the plant establishment process, labeled S1 through S4. The first stage, S1, represents dormant seeds. That is, seeds in this class have not yet germinated, but are still viable. Seeds in the second class are those that have germinated, but not yet emerged. The third stage represents plants that have emerged, and S4 symbolizes growing seedlings. Figure 1 shows a representation of this process.

The matrix U is written as

$$\begin{pmatrix} p_{11} & 0 & 0 & 0 \\ p_{21} & p_{22} & 0 & 0 \\ 0 & p_{32} & p_{33} & 0 \\ 0 & 0 & p_{43} & p_{44} \end{pmatrix}.$$

Note that the "Dead" compartment in the diagram does not show explicitly in the matrix formulation. This compartment is represented
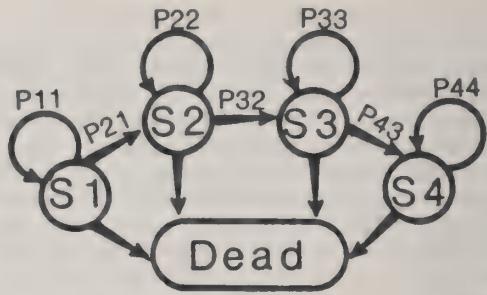
Figure 1. Transition diagram of plant biography.

implicitly, however. There are three pathways associated with each phase except Stage 4: remaining alive in the stage, passing on to the next stage, and dying. If the two probabilities associated with each compartment sum to unity, then there is no death. However, if they sum to less than unity, the remaining probability is assigned to mortality. Therefore,

$$\mu_i = 1 - p_{ii} - p_{ji},$$

where μ_i equals the probability that a plant will die in each stage (i) during the present time-step. Also, there is no fecundity explicit in the above matrix. The only stage that produces seeds is S4, the established plant. Placing a fecundity value f_4 in row 1 and column 4 of the matrix U would cause an incremental seed production each time step. The seasonal nature of plant propagule production nullifies the need to account for fecundity within this formulation and the SPUR model will calculate the production of new seeds. When seeds are produced, they will be added to the $n_1(t)$ component of the column vector $N(t)$ as follows:

$$\begin{pmatrix} n_1(t) + n_s \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}$$

where n_s is the number added to the seed population at time-step t. At most time steps, n_s will equal zero.

Given the definitions of S1 through S4, the probability values can now be defined:

$p_{11} \equiv$ probability that a dormant seed is alive at time (t+1) given that it was alive at time (t)

$p_{21} \equiv$ probability that a dormant seed germinates during time-period (t)

$p_{22} \equiv$ probability that a germinated seed is alive and its cotyledons have not extended at time (t+1) given the same condition at time (t).

$p_{32} \equiv$ probability that a germinated seed "emerges" (extends its cotyledons) during

time (t)

p_{33} ≡ probability that an emerged plant survives from time (t) to time (t+1)

p_{43} ≡ probability that an emerged plant begins primary growth in time-period (t)

p_{44} ≡ probability that an established seedling survives from time (t) to time (t+1).

As described above, to arrive at the number of plants in each category at time (t), the vector $N(t)$ will be updated at each time-step via left-multiplication by the matrix U:

$$N(t+1) = U \cdot N(t).$$

The two probabilities associated explicitly with each state are calculated as follows. Let p_{ji}' be the maximum potential probability of going from stage i to stage j in any time-period (t), and let $\xi_{ji}(t)$ be a function between zero and one that represents the proportion of p_{ji}' actually realized at time (t). Then,

$$p_{ji} = p_{ji}' \cdot \xi_{ji}(t).$$

The probability of staying in any state (i) and remaining viable, p_{ii}, can be calculated in a similar manner. Let

$$p_{ii}' = 1 - p_{ji},$$

where p_{ii}' equals the maximum value attainable by p_{ii} in a particular time-period. Then,

$$p_{ii} = (1 - p_{ji}) \cdot \xi_{ii}(t),$$

where $\xi_{ii}(t)$ is a function between zero and one that represents the proportion of p_{ii}' actually attained at time (t). The the probabilities p_{ji}, p_{ii} and the implicit μ_i all must sum to unity or, rearranging,

$$\mu_i = 1 - p_{ji} - p_{ii}$$

When the function $\xi_{ii}(t)$ equals one, then p_{ii} attains its maximum $(1 - pji)$ and μ_i equals zero:

$$\begin{aligned}\mu_i &= 1 - p_{ji} - p_{ii} \\ &= 1 - pji - (1 - pji) \\ &= 0.\end{aligned}$$

Thus, process rates for moving to stage j from stage i (p_{ji}) are calculated by reducing maximum rates (p_{ji}') by nondimensional-scalar multipliers ranging from 0 to 1 (ξ_{ji}). The shape of the response surfaces for the various processes will be obtained from the literature or by deducing the expected effect. This technique may, however, lead to over-reduction of some of the processes when several controlling factors are suboptimal (Detling et al. 1978) and the interactions between those factors are not clearly understood.

To solve the model, values for ξ_{ij} must be determined for each time step. The driving variables used to estimate these parameters are

shown in Table 1. The variables we selected were such that information is known to exist that describes the responses of the process p_{ij} to the factors contained within ξ_{ij}. Yet, we know that other variables are important in controlling the processes p_{ij}. With this in mind, random variables will be included within the model framework to approximate the effects of such factors as predation, soil structure, and herbivore activity (trampling of seedlings).

Table 1. List of factors needed to calculate parameters ξ_{ij}.

Parameter	Factors
ξ_{11}	Soil Temperature Soil Moisture
ξ_{21}	Soil Temperature Soil Moisture Solar Radiation

ξ_{22}	Soil Temperature
	Soil Moisture
	Seed Depth
	Pre-emergent
	    Herbicide
	    Concentration

ξ_{32}	Soil Temperature Soil Moisture
ξ_{33}	Soil Temperature Soil Moisture Nutrients
ξ_{43}	Soil Temperature Soil Moisture Solar Radiation Nutrients

ξ_{44}	Soil Temperature
	Soil Moisture
	Seed Density
	Post-emergent
	    Herbicide
	    Concentration

The factors used in the model are well known to affect the germination and development of seedlings. Soil-surface temperature and soil moisture are the most prominent variables that control the developmental biography of plants (Asana and Williams 1965, Black 1970, Campbell and Read 1968, Sofield 1977, Warrington et al. 1977). Nitrogen and phosphorus are also very important in the development of seedlings, but primarily influence the later stages of plant development (Black 1970, Blackman and Rutter 1947). We are assuming that sufficient nutrient reserve exists in the seed to drive germination and emergence (Bannister 1976). Solar radiation is important for primary growth and for the germination of some plants (Friend 1965, Friend et al. 1963, Wall 1974, Wardlaw 1970). Seed

depth at time of germination is important in determining the probability of the survival of the post-germination embryo (Horn and Leu 1978, Robocker et al. 1969, Beveridge and Wilsie 1959, Evans and Young 1972). If the seed is planted too deep, energy stored within the seed is insufficient for the hypocotyl to reach the soil surface. If the seed is not planted deep enough, the plant will not have an adequate rooting zone to anchor the plant and to subsequently extract necessary water. Both scenarios result in death to the seedling. Seed density also affects the survivability of seedlings (Benjamin 1982, Baker and Briggs 1983, Fowler 1984, Glendening 1941, McGinnies 1978, Vassey et al. 1985). Herbicides often are used in establishing new plantings on range- and croplands (Eckert 1974, Eckert et al. 1974, Young and Evans 1972). Pre-emergent and post-emergent herbicides should be considered within the model structure.

DISCUSSION

A comprehensive understanding of rangeland-production systems includes the competition of multiple plant species and their intrinsic interactions, the heterogeneity of range sites, and the analysis of many other simultaneous processes that control native-plant community dynamics. Mathematical modeling seems a logical method for identification, interpretation, and management of the biotic and abiotic influences governing rangeland systems and to support on-going empirical research.

The model outlined in this paper is a simple yet powerful construct to describe early plant biography. The next step in model construction will be to develop the functions ξ_{ii} and ξ_{ii} that modify the probabilities p_{ii} and p_{ii}, respectively. As described above, the equations will be functions of environmental variables such as soil temperature and moisture, solar radiation and nutrient availability. The functional forms of such individual effects are not difficult to arrive at from the literature. There are difficulties, however, because these variables interact in ways that are not always obvious. An interaction occurs when, for factors α and β, the response of the dependent variable y to different values of β changes with different values of α. Experiments must be designed to quantify the interactions of the various factors used within the model and to investigate not only linear, but nonlinear model formulations. In a future paper we will present the functional forms needed for designing experiments that will adequately parameterize this model.

The colonization model is being designed to work in concert with the SPUR rangeland simulation, and will bring an added dimension to that model. Because of the simple input required, it will also be easily adaptable to other simulation models where colonization representation is desirable. As a stand-alone model, it will be useful in the analysis of rangeland revegetation following overgrazing and other disturbances such as fire.

The scientific community must begin incorporating general systems thinking into experimental design. In other words, we should not focus narrowly on individual processes, but place them into the context of the entire ecological system. For example, experimental designs should elucidate the effect of factor interactions on germination rate by utilizing a complete range of temperatures, water potentials, and nutrient levels. We must begin to study the various rangeland processes holistically. By understanding how individual components interact and affect the system as a whole, great progress will be made in understanding range ecology.

LITERATURE CITED

Anderson, M.C. 1966. Ecological groupings of plants. Nature (London) 212:54-56.

Asana, R.D. and R.F. Williams. 1965. The effect of temperature stress on grain development in wheat. Aust. J. Agric. Res. 16:1-13.

Baker, R.J. and K.G. Briggs. 1983. Relationships between plant density and yield in barley. Crop Sci. 23:590:592.

Bannister, P. 1976. Introduction to Physiological Plant Ecology. John Wiley & Sons, New York. 273 pp.

Benjamin, L.R. 1982. A model to predict the effects of complex row spacing on the yields of root crops. J. Agric. Sci., Cambridge 98: 131-139.

Beveridge, J.L. and C.D. Wilsie. 1959. Influence of depth of planting, seed size, and variety on emergence and seedling vigor in alfalfa. Agron. J. 51:731-734.

Black, A.L. 1970. Soil water and soil temperature influences on dryland winter wheat. Agron. J. 62:797-801.

Blackman, G.E. and A.J. Rutter. 1947. Physiological and ecological studies in the analysis of plant environment. II. The interaction between light intensity and mineral nutrient supply in the growth and development of the bluebell (Scilla non-scripta). Annals of Bot. 11:125-158.

Bould, A. and B.K. Abrol. 1981. A model for seed germination curves. Seed Sci. and Techn. 9:601-611.

Campbell, C.A. and D.W.L. Read. 1968. Influence of air temperature, light intensity and soil moisture on the growth, yield and some growth analysis characteristics of chinook wheat grown in the growth chamber. Can. J. Plant Sci. 48:299-311.

Carmer, S.G. and J.A. Jackobs. 1965. An exponential model for predicting optimum plant density and maximum corn yield. Agron.

J. 57:241-244.

Detling, J.K., W.J. Parton, and H.W. Hunt. 1978. An empirical model for estimating CO_2 exchange of Bouteloua gracilis (H.B.K.)Lag. biomass in shortgrass prairie. Oecologia (Berl.) 33:137-147.

Eckert, R.E., Jr. 1974. Atrazine residue and seedling establishment in furrows. J. Range Manage. 27:55-56.

Eckert, R.E., Jr., J.E. Asher, M.D. Christensen, and R.A. Evans. 1974. Evaluation of the atrazine-fallow technique for weed control and seedling establishment. J. Range Manage 27:288-292.

Evans, R.A. and J.A. Young. 1972. Microsite Requirements for establishment of annual rangeland weeds. Weed Sci. 20: 350-356.

Fowler, N.L. 1984. The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in Linum. J. Ecol. 72: 307-318.

Frasier, G.W. 1986. Water requirements for rangeland plant establishment. Water Forum '86: World Water Issues in Evolution. ASCE Conf., Long Beach, CA.

Friend, D.J.C. 1965. Ear length and spikelet number of wheat grown at different temperatures and light intensities. Can. J. Bot. 43:345-353.

Friend, D.J.C., J.E. Fisher, and V.A. Helson. 1963. The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. Can. J. Bot. 41:1663-1674.

Glendening, G.E. 1941. Development of seedlings of Heteropogon contortus as related to soil moisture and competition. Bot. Gaz. 102:684-698.

Goloff, A.A., Jr. and F.A. Bazzaz. 1975. A germination model for natural seed populations. J. Theor. Biology 52: 259-283.

Hanson, J. D., W.J. Parton, and G.S. Innis. 1985(a). Plant growth and production equations for grassland ecosystems: A comparison of modelling approaches. Ecol. Mod. 29:131-144.

Hanson, J. D., J.W. Skiles, and W.J. Parton. 1985(b). A rangeland plant production model. Pages 252-257 in: D.G. DeCoursey (ed.), Proceedings of the Natural Resources Modeling Symposium. USDA-ARS Publication ARS-30. 496 p.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.

Horn, H.S. 1975. Forest succession. Sci. Amer. 232:90-98.

Horng, L.C. and L.S. Leu. 1978. The effects of depth and duration of burial on the germination of ten annual weed seeds. Weed Sci. 26:4-10.

Hsu, F.H., C.J. Nelson, and W.S. Chow. 1984. A mathematical model to utilize the logistic function in germination and seedling growth. J. Exp. Bot. 35:1629-1640.

Knisel, W. G., ed. 1980. CREAMS: A Field-Scale Model for Chemicals, Runoff, and Erosion from Agricultural Management Systems. U.S. Department of Agriculture, Conservation Research Report No. 26. 640 pp.

Lane, L. J. 1985. Hydrological and sediment transport processes in ephemeral stream channels: Component of the SPUR model. Pages 360-365 in: D.G. DeCoursey (ed.), Proceedings of the Natural Resources Modeling Symposium. USDA-ARS Publication ARS-30. 496 p.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

McGinnies, W.J. 1978. Thinning of blue grama range for increased seed and forage production. Proceedings of the First International Rangeland Congress. Soc. Range Manage., Denver, CO. P. 645-646.

Olson, R.L., Jr., P.J.H. Sharpe, and H. Wu. 1985. Whole-plant modeling: a continuous-time Markov approach. Ecol. Mod. 29:171-187.

Pacala, Stephen W. and J.A. Silander, Jr. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. Am. Nat. 125:385-411.

Rice, R.W., M.D. MacNeil, T.G. Jenkins, and L.J. Koong. 1983. Emulation of the herbage/animal interface of grazinglands. Pages 475-488 in: W.K. Lauenroth et. al. (eds.), Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling. Elsevier Scientific Publishing Co., New York. 992 p.

Richards, F.J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

Robocker, W.C., W.C. Williams, R.A. Evans, and R.J. Torell. 1969. Effect of age, burial, and region on germination and viability of Halogeton seed. Weed Sci. 17:63-65.

Sanders, J. O. and T. C. Cartwright. 1979. A general cattle production systems model. I. Description of the model. Agric. Sys. 4:217-227.

Schimpf, D.J., S.D. Flint, and I.G. Palmblad. 1977. Representation of germination curves with the logistic function. Ann. Bot. 41:1357-1360.

Sharpe, Peter P.J.H and D.W. DeMichele. 1977. Reaction kinetics of poikilotherm develoment. J. Theor. Biology 54:649-670.

Sharpe, P.J.H., J. Walker, L.K. Penridge, and H. Wu. 1985. A physiologically based continuous-time Markov approach to plant growth modelling in semi-arid woodlands. Ecol. Mod. 29:189-213.

Skiles, J.W., J.D. Hanson, and W.J. Parton. 1983. Simulation of above- and below-ground carbon and nitrogen dynamics of Bouteloua gracilis and Agropyron smithii. Pages 467-473 in: W.K. Lauenroth et. al. (eds.), Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling. Elsevier Scientific Publishing Co., New York. 992 p.

Sofield, L.T., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4:785-797.

Springer, E.P., C.W. Johnson, K.R. Cooley, and D.C. Robertson. 1984. Testing the SPUR hydrology component on rangeland watersheds in southwest Idaho. Transactions of ASAE 27:1040-1046, and 1054.

Thornley, J.H.M. 1977. Germination of seeds and spores. Ann. Bot. 41:1363-1365.

Thornley, J.H.M. 1983. Crop yield and planting density. Ann. Bot. 52:257-259.

Usher, M.B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. J. of Appl. Ecol. 3:355-367.

Vassey, T.L., J.R. George, and R.E. Mullen. 1985. Early-, mid-, and late-spring establishment of switchgrass at several seeding rates. Agron. J. 77:253-257.

Waggoner, P.E. and J.Y. Parlange. 1974. Mathematical model for spore germination at changing temperature. Phytopathol. 64:6-05-610.

Wall, P.C., and P.M. Cartwright. 1974. Effects of photoperiod, temperature and vernalization on the phenology and spikelet numbers of spring wheats. Ann. Appl. Biology 76:299-309.

Wardlaw, I.F. 1970. The early stages of grain development in wheat: Response to light and temperature in a single variety. Aust. J. Biol. Sci. 23:765-774.

Warrington, I.J., R.L. Dunstone, and L.M. Green. 1977. Temperature effects at three development stages on the yield of the wheat ear. Aust. J. Agric. Res. 28:11-27.

Wight, J.R. (ed). 1983. SPUR--Simulation of Production and Utilization of Rangelands: A Rangeland Model for Management and Research. USDA Misc. Publ. 1431. 120 p.

Williams, J.R. 1975. Sediment-yield prediction with Universal Equation using runoff energy factor. Pages 244-252 in: Present and Perspective Technology for Predicting Sediment Yield and Sources. USDA, ARS-S-40.

Williams, J.R., P.T. Dyke, and C.A. Jones. 1983. EPIC--A model for assessing the effects of erosion on soil productivity. Pages 553-572 in: Lauenroth et al. (eds.), Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling. Development in Environmental Modelling 5. Elsevier Scientific Publishing Company. Amsterdam. 992 pp.

Williams, W.T., G.N. Lance, L.J. Webb, J.G. Tracey, and M.B. Dale. 1969. Studies in the numerical analysis of complex rain-forest communities III. The analysis of successional data. J. Ecol. 57: 515-535.

Wilson, L.T. and W.W. Barnett. 1983. Degree-days: an aid in crop and pest management. Calif. Agric. 37:4-7.

Wu., H., P.J.H. Sharpe, J. Walker, and L.K. Penridge. 1985. Ecological field theory: a spatial analysis of resource interference among plants. Ecol. Mod. 29:215-243.

Young, J.A. and R.A. Evans. 1972. Conversion of medusahead to downy brome communities with diuron. J. Range Manage. 25:40-43.

SUSCEPTIBILITY OF ANTELOPE BITTERBRUSH TO SEEDBED DAMPING-OFF DISEASE

David L. Nelson[1]

ABSTRACT

Seed and seedlings of five bitterbrush accessions tested moderately to highly susceptible to Fusarium, Pythium, and Rhizoctonia, fungi known to induce damping-off disease. The Mono County, California accession showed less susceptibility than others. Two bitterbrush seedborne fungi (Sphaeropsis and Sclerotium) destroyed all seedlings from eight bitterbrush accessions.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata [Pursh] DC.) is of interest in the management of Western United States rangelands (Basile 1967, Guinta et al. 1978, Clark and Britton 1979) because of its palatability and nutritive value as browse (Leach 1956, Kufeld et al. 1973, Tueller 1979, Bartmann 1983). Most bitterbrush restoration experimentation has been on practical methods of establishment and rejuvenation of existing stands (Holmgren 1954, Brown and Martinsen 1959, Hubbard 1964, Plummer et al. 1968, Ferguson 1972, Tiedemann and Johnson 1983). Seed dormancy and germination (Mirov and Kraebel 1937, Hormay 1943, Young and Evans 1976) and seedling plant competition (Holmgren 1956, Hubbard 1957) have been important obstacles to bitterbrush planting and establishment. The role of pathogenic microorganisms as a detrimental factor during these phases has been given only cursory consideration.

During seed stratification and germination tests on antelope bitterbrush, Peterson (1953) noted severe "seed spoilage." McHenry and Jensen (1967) found "Rhizopus and other saprophytic fungi common throughout" their seed germination tests. Reduced germination, following prolonged stratification, was apparently caused partially by "microbial rot," in seed germination studies by Young and Evans (1976). "Damping-off" type symptoms in germination tests (Peterson 1953) and in field plantings (Holmgren 1956, Brown and Martinsen 1959) have been reported. Nord (1965) reported controlled tests in which Rhizoctonia DC. ex Fr. and Pythium Pringsh. species (common damping-off pathogens) caused severe seedling mortality. Fusarium, Link ex Fr., Rhizoctonia and especially Pythium have all been isolated from bitterbrush seedlings with damping-off symptoms from material sent to the Intermountain Station's Shrub Sciences Laboratory from the Forest Service, Intermountain Region, Lucky Peak Nursery in Idaho by Nancy Shaw (Intermountain Research Station, Boise, Idaho).

---

[1] Research Plant Pathologist, USDA Forest Service, Intermountain Research Station, Shrub Sciences Laboratory, 735 North 500 East, Provo, Utah 84601.

Damping-off is a disease of young seedlings. Infection usually begins just below the soil level on the upper portion of taproots or lower hypocotyl. Seedlings are most susceptible during rapid early growth when plant tissue is primarily parenchymatous, prior to formation of lignified or suberized cell walls and secondary fibrovascular cambial activity. With rapid pathogen invasion and killing of cells, root or hypocotyl tissues collapse and the seedling falls over near the soil line. The hypocotyl appears water soaked or rotted and shrunken with a darkened discoloration. In general, cool and moist conditions are conducive to damping-off induced by Pythiaceous fungi and slightly warmer and drier conditions for Rhizoctonia and Fusarium related damping-off or root rot.

In containerized greenhouse production of bitterbrush, losses from damping-off are commonly encountered. Severe loss with certain seed sources has resulted from some greenhouse operations (T. D. Landis, B. M. Tkacz, Forest Service, Regions 2 and 4, unpublished observations). Restriction of mortality to certain seed sources suggests the possibility of varied host susceptibility to soilborne fungi or existence of seedborne pathogens. Species of Sclerotium Tode ex Fr. and Sphaeropsis Sacc. have been isolated from bitterbrush seed accessions from seven Western States and are implicated as inducers of seedling damping-off (Nelson 1985).

The objective of this study was to evaluate through controlled experimentation the potential susceptibility of bitterbrush seed and seedlings to a range of damping-off type fungi.

MATERIALS AND METHODS

Material Source and Seed Preparation

Test specimen isolates of damping-off pathogens were obtained from various sources (Fusarium, P. E. Nelson, Fusarium Research Center, Pennsylvania State University, College Park; Pythium, M. E. Stanghellini, Department of Plant Pathology, University of Arizona, Tucson; Rhizoctonia, E. E. Butler, Dept. of Plant Pathology, University of California, Davis; Sclerotium and Sphaeropsis, USDA Forest Service, Shrub Sciences Laboratory, Provo, Utah). Selection of fungus isolates was based on a known history of pathogenicity--on pine seedlings from forest nurseries, on root systems of rangeland shrub species, on agricultural plants, and seedborne on bitterbrush.

Bitterbrush seed accessions were obtained from private seed companies, USDA Forest Service, Utah Division of Wildlife Resources, Nevada State Division of Forestry, and Bureau of Land Management. The objective was broad geographical representation.

Seeds were prepared for tests by: leaching for 24 h with cold running tap water to soften seed coats and reduce possible germination inhibitors; shaking in 250 mL flasks on a rotary shaker at 200 r/min for 10 min in 10.0 percent bleach (5.0 percent NaClO) and a drop of surfactant to reduce seed surface-borne fungi; rinsing with five changes of sterile water to remove sodium; and stratifying between moist filter paper in Petri dishes for 60 days at 1 °C to enhance germination rate and vigor. Eighteen seed accessions were screened for presence of internal seed-coat-borne fungi. This was done by plating 50 stratified seeds per accession on potato-dextrose agar (PDA) in Petri dishes and incubating in the laboratory at 20 to 22 °C and a 12 h photoperiod for 2 weeks. Only five accessions were found free of seed-coat borne fungi and three had less than a 3.0 percent infestation rate. These accessions were used for the pathogenicity tests.

Pathogenicity Tests

Test fungi were maintained on either PDA (Fusarium, Rhizoctonia, Sphaeropsis, Sclerotium) or V8 agar (puree of eight vegetables) (Pythium) culture medium. Seven-day old cultures were used for inoculum. Damping-off pathogenicity tests were made by two methods:

1. Samples of five stratified seeds per Petri dish were plated on 2 percent water agar. Inoculatations were made by placing an agar culture cube (3 mm) of the test fungus adjacent to each seed. The treatments for each fungus and seed source were replicated 10 times. The inoculation test plates were incubated in the laboratory at 20 to 22 °C and a 12 h day-night lighting cycle.

2. Samples of 10 seeds were planted in sterile, washed sand in 3-inch (3.75-cm) pots and inoculated with five cubes (3 mm) of fungus agar culture. This test was replicated five times for each seed and fungus source. The test was incubated in the laboratory as described above.

The tests were observed for disease symptoms 14 days after inoculation. Sclerotium and Sphaeropsis were tested by method 1, while Fusarium, Pythium, and Rhizoctonia were tested by method 2. To confirm induction of damping-off by the inoculated fungus isolate, up to five seedlings with symptoms were plated on PDA medium in Petri dishes for each treatment-bitterbrush accession combination. Any recovered fungi were checked for identity.

Analysis of variance was used to test for difference among treatments.

RESULTS AND DISCUSSION

With all treatment-bitterbrush accession combinations, the inoculated fungus isolate was recovered from damping-off diseased plants. Seed and seedlings of all eight bitterbrush accessions tested were destroyed when exposed to the Sclerotium or Sphaeropsis seedborne fungal isolates (Table 1). Sphaeropsis appears to be less virulent in that more seedlings reached the cotyledonary stage before being killed than with

Table 1. Susceptibility of bitterbrush seedlings to damping-off disease induced by seedborne fungi of bitterbrush

Bitterbrush seed sources	Control percent survival[2]	Mean percent seed germination/Percent seedling survival[1]									
		Sphaeropsis isolates[3]					Sclerotium isolates[3]				
		1	2	3	4	5	1	2	3	4	5
Janesville, Calif.	72.0	40/0*[4]	28/0*	18/0*	34/0*	12/0*	6/0*	8/0*	14/0*	6/0*	24/0*
Mono Co., Calif.	74.0	64/0	70/0	74/0	72/0	68/0	66/0	74/0	52/0	64/0	66/0
Siskiyou Co., Calif.	96.0	82/0	70/0	78/0	72/0	64/0*	70/0	74/0	36/0*	48/0*	62/0*
Elko, Nev.	96.0	74/0	76/0	70/0	64/0	80/0	64/0	66/0	52/0*	62/0	54/0*
Washoe Valley, Nev.	86.0	88/0	78/0	84/0	80/0	82/0	78/0	78/0	64/0	68/0	80/0
Lakeview, Ore.	90.0	72/0	62/0	78/0	82/0	76/0	64/0	44/0*	26/0*	62/0	42/0*
Mt. Pleasant, Ut.	74.0	84/0	62/0	76/0	62/0	60/0	58/0	60/0	52/0	56/0	54/0
Lincoln Co., Wyo.	100.0	98/0	94/0	96/0	100/0	98/0	82/0	82/0	72/0*	74/0*	88/0

[1] Mean percentage seed germination and seedling survival 2 weeks after inoculation.
[2] Percentage survival of uninoculated control seedlings.
[3] Seedborne fungal isolates from bitterbrush (source origin).

Diplodia	Sclerotium
1. Lincoln Co., Wyo.	1. Lincoln Co., Wyo.
2. Soda Springs, Id.	2. Summit Pass, Id.
3. Orem, Ut.	3. Dillon, Colo.
4. Maybell, Colo.	4. Pioche, Nev.
5. Kemmerer, Wyo.	5. Kemmerer, Wyo.

[4] Seed mean germination percentages followed by an asterisk are significantly different than the control (within each bitterbrush seed source) α = 0.05, Tukey's Stutantized Range Test.

Table 2. Susceptibility of bitterbrush seedlings to various damping-off inducing test fungi

Fungus Isolates	Bitterbrush accession groups[1]				
	1	2	3	4	5
Uninoculated control	68.0[2] a[3] 10.7	70.0 a 6.3	72.0 a 11.6	60.0 a 9.0	82.0 a 8.5
Fusarium oxysporum 0-1-53	50.0 a 6.3	48.0 a 8.5	42.0 a 5.8	56.0 a 6.7	62.0 abc 8.0
F. oxysporum Sahlecht. emend. Snyd. & Hans. 0-1062	50.0 a 4.5	75.0 a 2.7 *[4]	48.0 a 7.2	52.0 a 3.6	46.0 bcd 6.7
F. oxysporum 0-1159	48.0 a 10.0	45.0 10.7	46.0 a 4.0	42.0 a 9.8	74.0 ab 5.8
F. culmorum (W.G. Smith) Sacc. R-5906	34.0 a 11.0	57.5 a 5.8	42.0 a 10.7	36.0 a 8.0	52.0 abcd 7.2
Pythium aphanidermatum (Edson) Fitzp.	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0
P. dissotocum Drechsler	54.0 a 8.5	65.0 a 4.5	58.0 a 4.9	58.0 a 3.6	68.0 ab 4.9
P. ultimum Trow.	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0
P. irregulare Buisman	0.0 0.0	0.0 0.0	0.0 0.0	8.0 b 3.6	4.0 e 2.2
P. catenulatum Matthews	62.0 a 6.7 *	0.0 0.0	0.0 0.0	6.0 b 2.8	20.0 de 8.9
Rhizoctonia solani Kuhn (43)	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0
R. solani (141)	40.0 a 9.0 *	0.0 0.0	0.0 0.0	2.0 b 1.8	0.0 0.0
R. solani (229)	46.0 a 8.5	52.5 a 11.6	50.0 a 3.1	40.0 a 0.0	32.0 cde 9.8
R. solani (283)	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0
R. solani (457)	32.0 a 7.2 *	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0
R. solani (465)	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0
R. solani (481)	60.0 a 8.5 *	0.0 0.0	0.0 0.0	0.0 0.0	6.0 e 2.2

[1]Bitterbrush seed accession origin: 1. Mono Co., Calif. 2. Janesville, Calif. 3. Mt. Pleasant, Ut. 4. Washoe Valley, Nev. 5. Lincoln Co., Wyo.
[2]Figures represent mean percentage survival two weeks after inoculation over the standard error of the mean.
[3]Means (within bitterbrush accession groups) followed by the same letter are not significantly different α =0.05, Tukey's Stutentized Range Test. Bitterbrush accessions having no survival within bitterbrush groups were not included in the multiple range test.
[4]Means with asterisk are significantly different than others within fungus isolate groups.

Sclerotium. Also with Sclerotium more seeds were killed prior to radicle emergence. The important result, however, is that no seedlings survived. In the sand culture tests, bitterbrush accessions were clearly less susceptible to the Fusarium isolates than most Pythium and Rhizoctonia isolates (Table 2). There was no clear difference is susceptibility of bitterbrush to the various Fusarium isolates. With the exception of Pythium dissotocum, the Pythium isolates were highly virulent to bitterbrush seedlings. A notable exception was the apparent resistance of the Mono County, California bitterbrush accession to P. catenulatum. In general, Rhizoctonia solani was also highly virulent to bitterbrush seedlings. R. solani (229) was least virulent. The Mono County accession showed evidence of resistance to R. solani accession (229) and also accesions (141), (457), and (481).

Mono County, California is a transitional zone between northern populations of Purshia tridentata and southern populations of Purshia glandulosa Curran (desert bitterbrush) where the two species intergrade (Nord 1965). Whether P. glandulosa genetic influence imparts more resistance to damping-off is perhaps worth testing.

SUMMARY AND CONCLUSIONS

From these results it is clear that antelope bitterbrush is highly susceptible to a wide range of damping-off type fungi. These results are not unusual and may be expected with most plant seedlings exposed to this class of soilborne fungi. Perhaps the greatest danger is from the two seedborne fungi tested. Their occurrence is widespread, and they can be in a high percentage of seeds (Nelson 1985).

Evaluation based on pure culture laboratory pathogenicity tests should be considered potential in nature. Environmental conditions are generally optimal for the pathogen, and the results cannot be directly extrapolated to field situations. Occurrence of a disease depends on an interaction of the host plant, pathogenic agent, and a conducive environment. In a naturally balanced soil flora, there is usually competition as well as antagonism from other microorganisms that tend to suppress pathogenic types. Examples of pathogen antagonists are Bacillus subtilis, certain actinormycetes, and fungi such as Trichoderma Pers. ex Fr., Gliocladium Corda, and Penicillium Link ex Fr. The function of these organism is influenced by soil factor such as soil water potential, pH, nutrients, temperature, and soil type. Therefore biological suppression of damping-off depends on the presence of a soil environment more conducive to the antagonist than to the pathogen (Cook and Baker 1983). It is in the poorly balanced flora of nursery soils and greenhouse plant growing mediums where the risk is higher for damping-off disease problems.

A program of pathogen-free seed certification, seed treatment, and proper management of greenhouse and nursery soil environment needs to evolve with the emerging wildland shrub industry to avoid seedbed plant disease problems (Nelson 1984).

LITERATURE CITED

Basile, J. V. 1967. An annotated bibliography of bitterbrush (Purshia tridentata [Pursh] DC). USDA For. Serv. Res. Pap. INT-44, 27 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Bartmann, R. M. 1983. Composition and quality of mule deer diets on pinyon-juniper winter range, Colorado. J. Range Manage. 34:534-541.

Brown, R. B., and C. F. Martinsen. 1959. Browse planting for big game in the state of Washington. Biol. Bull. 12, 63 p. Washington State Game Dep., Olympia, Wash.

Clark, R. G., and C. M. Britton. 1979. A bibliography of bitterbrush annotated from 1967-1978. Bull. 690, 18 p. Oregon Agric. Exp. Stn., Corvallis, OR.

Cook, R. J., and K. F. Baker. 1983. The nature and practice of biological control of plant pathogens. 539 p. The American Phytopathological Society, St. Paul, Minn.

Ferguson, R. B. 1972. Bitterbrush topping: shrub response and cost factors. USDA For. Serv. Res. Pap. INT-125, 11 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Guinta, B. C., R. Stevens, K. R. Jorgensen, and A. P. Plummer. 1978. Antelope bitterbrush--an important wildland shrub. Publ. No. 78-12, 48 p. Utah Div. Wildlife Resources, Salt Lake City, Utah.

Holmgren, R. C. 1954. A comparison of browse species for revegetation of big game winter ranges in southeastern Idaho. USDA For. Serv. Res. Pap. 33, 3 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Holmgren, R. C. 1956. Competition between annuals and young bitterbrush (Purshia tridentata) in Idaho. Ecology 37:370-377.

Hormay, A. L. 1943. Bitterbrush in California. USDA For. Serv. Res. Note 34, 12 p. Calif. For. and Range Exp. Stn., Berkeley, Calif.

Hubbard, R. L. 1957. The effects of plant competition on the growth and survival of bitterbrush seedlings. J. Range Manage. 10:135-137.

Hubbard, R. L. 1964. A guide to bitterbrush seeding in California. 30 p. USDA For. Serv., Pacific Southwest For. and Range Exp. Stn., and Calif. Dept. Fish and Game Resour. Agency, Berkeley, Calif.

Kufeld, R. C., O. C. Wallmo, and C. Feddema. 1973. Foods of the Rocky Mountain mule deer. USDA For. Serv. Res. Pap. RM-111, 31 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Leach, H. R. 1956. Food habits of the Great Basin deer herds of California. California Fish and Game 42:243-308.

McHenry, W. B. and L. A. Jensen. 1967. Response of bitterbrush (Purshia tridentata) seed to certain germination methods. Proc. Assoc. Off. Seed Anal. 57:89-95.

Mirov, N. T., and C. T. Kraebel. 1937. Collecting and handling the seeds of California wild plants. USDA For. Serv. Res. Note 18, 27 p. Calif. For. and Range Exp. Stn., Berkeley, Calif.

Nelson, D. L. 1984. Toward producing disease-free container-grown native wildland plants. Pages 32-37 In: Patrick M. Murphy, compiler. The challenge of producing native plants for the Intermountain area. Proceedings: Intermountain Nurseryman's Association 1983 Conference. USDA For. Serv. Gen. Tech. Rep. INT-168, 96 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Nelson, D. L. 1985. Seedborne fungal pathogens of bitterbrush (Purshia tridentata). Phytopathology Abstr. 75:1368.

Nord, C. E. 1965. Autoecology of bitterbrush in California. Ecological Monographs 35:307-334.

Peterson, R. A. 1953. Comparative effect of seed treatments upon seedling emergence in seven browse species. Ecology 34:778-785.

Plummer, A. P., D. R. Christensen, and S. B. Monsen. 1968. Restoring big game range in Utah. Publ. No. 68-3, 183 p. Utah Div. Fish and Game, Salt Lake City, Utah.

Tiedemann, A. R., and K. L. Johnson, compilers. 1983. Proceedings--research and management of bitterbrush and cliffrose in western North America. USDA For. Serv. Gen. Tech. Rep. INT-152, 279 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Tueller, P. T. 1979. Food habits and nutrition of mule deer on Nevada ranges. Univ. of Nevada, Nevada Agriculture Exp. Stn., 104 p.

Young, J. A., and R. A. Evans. 1976. Stratification of bitterbrush seeds. J. Range Manage. 29:421-425.

SEED AND SEED PATCH USE BY THREE
HETEROMYID RODENT SPECIES

William S. Longland[1]

ABSTRACT

Two species of kangaroo rats showed distinct
preferences for particular seeds when offered a
choice of seeds from four plant species occurring
in the rodents' native habitat. These kangaroo
rats and a pocket mouse also preferred particular
artificial seed patches which differed in seed
distributions and edaphic features. The nonrandom
patterns of seed and seed patch use exhibited by
these rodents may be important determinants of
distributions and abundances of range plants.

INTRODUCTION

Granivorous (i.e., seed-eating) animals can have
substantial effects on the distribution and
abundance of seeds, and consequently on adult
plants as well (Brown et al. 1979, Rissing 1986,
Price and Jenkins 1987). They affect distribution
by moving and caching (i.e., storing) seeds. They
reduce seed densities by consumption and by
caching in microsites that do not permit
germination or establishment. Price and Jenkins
(1987) detail the numerous pathways through which
granivores can influence seed fate.

In deserts and other arid areas, which are
depauperate in palatable foliage, and where many
ephemeral plant species occur only in the form of
seeds for extended periods, granivory may have an
especially pronounced impact on seed densities
and distributions, and thus on the plant
community as a whole. This has important
implications for managers of desert rangelands.
Many desert ephemerals provide desirable forage
for rangeland livestock and wildlife. Range
improvements often involve the seeding of exotic
plants for forage, such as crested wheatgrass
(Agropyron spp.), which are phylogenetically
"inexperienced" with local granivore fauna. On
the other hand, desirable or undesirable native
range plants may depend on local granivores for
seed dispersal. Appropriate management programs
for such plant species are likely to require an
understanding of plant/granivore interactions.

Three groups of potentially important granivores
occur in the arid southwestern United States:
ants, birds, and rodents. Birds are, for all
practical purposes, only seed predators, because
the seeds they glean from the soil surface are
eaten upon collection (Brown et al. 1979). A
notable exception is provided by birds of the
family Corvidae, many of which cache large
numbers of pine tree (Pinus spp.) seeds (Vander

Wall and Balda 1977, Tombak 1982). Desert rodents
and harvester ants act as both predators and
dispersers of seeds. As a general rule rodents
take larger seeds than ants (Brown et al. 1979),
however there is a great deal of overlap: rodents
utilize seeds >0.25 mg (Price and Reichman 1987),
whereas ants utilize seeds $\leq$1.5 mg (Rissing
1981). Considerable evidence suggests that this
overlap is sufficient to facilitate resource
competition between these distantly related taxa
(Brown and Davidson 1977, Davidson et al. 1980).
Although preferred seed sizes of ants and rodents
overlap, these granivores differ in many other
respects.

The vast majority of ant-collected seeds are
placed in granaries within ant colonies and thus
removed from the germinable seed pool. The only
seeds escaping ant predation are those deposited
in refuse piles near colony entrances (Rissing
1986). Ant activity apparently enhances the
probability of germination for some plant
species' seeds, but impairs other plants (Rissing
1986). Rodents also cache seeds in a centrally-
located burrow, but often make a number of
scattered caches ("scatterhoards") just below the
soil surface. Unrecovered scatterhoards provide
a mechanism for recruitment of new plants (Price
and Jenkins 1987) and since they occur throughout
rodent home ranges, they are not as spatially
restricted as new plants germinating outside of
dispersed ant colonies.

Another important difference among granivore taxa
is that ants and birds gather their seeds from
the soil surface, while rodents dig for buried
seeds as well as taking surface seeds (Brown et
al. 1979, Price and Jenkins 1987). Furthermore,
non-hibernating rodents harvest seeds year-round;
ants and birds are seasonal granivores (Pulliam
and Brand 1975). For these reasons, rodents
probably have the strongest potential for
affecting arid rangeland plant communities
through granivory. Indeed, desert rodents may
harvest >75% of an entire seed crop (Chew and
Chew 1970, Nelson and Chew 1977, Borchert and
Jain 1978, Brown et al. 1979, Price and Jenkins
1987). The fate of these seeds following harvest
must be an important determinant of recruitment
in plant populations. For example, Batzli and
Pitelka (1970) and Borchert and Jain (1978) used
exclosures to show that rodents can remove the
majority of seeds of preferred plant species, and
that densities of these plants can be reduced by
>60% on plots with rodents relative to control
plots. These results underscore the potential
influence of rodent foraging preferences on range
plant populations.

The most specialized granivorous rodents in North
American deserts belong to the family
Heteromyidae. Heteromyids frequently comprise a
substantial proportion of rodent species
assemblages in desert habitats. They feed almost

[1]Graduate Student/Research Assistant,
 Department of Biology, University of California,
 Riverside, California 92521.

exclusively on seeds; other desert rodents eat insects and vegetative material as well. They are very efficient at locating and harvesting seeds. They have external cheek pouches permitting collection and movement of large quantities of seeds per foraging bout. They also cache large quantities of seeds in burrows and in shallow scatterhoards. Not all of their caches are recovered for consumption, and consequently some caches germinate (Price and Jenkins 1987). Caching activity by heteromyids may even enhance the probability of germination for seeds of some range plants (Reynolds and Glendening 1949, Reynolds 1950, LaTourrette et al. 1971, McAdoo et al. 1983). A detailed understanding of how heteromyid foraging activities may affect seeds in nature is likely to require knowledge of the animals' natural histories.

Assemblages of coexisting heteromyid species in the American southwest are among the most thoroughly studied communities of terrestrial vertebrates. A consistently documented pattern in heteromyid communities involves a relationship between locomotory gait and foraging microhabitat: quadrupedal pocket mice (_Perognathus_ spp.) use areas beneath and around shrub canopies, whereas bipedal kangaroo rats (_Dipodomys_ spp.) and kangaroo mice (_Microdipodops_ spp.) forage primarily in open spaces between perennial vegetation (cf. Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Price 1978, Bowers 1982, Harris 1984, 1986). One hypothesis attempting to explain this correlation between morphology and foraging behavior suggests that biomechanical aspects of bipedalism and quadrupedalism favor seed harvest in open and shrub microhabitats, respectively. Support for this possibility comes from evidence that open and shrub microhabitats differ in seed species composition, seed distibution patterns, soil density, and soil texture (Price and Waser 1985, Price and Reichman 1987). Four heteromyid species which coexist in southeastern Arizona preferred artificial seed patches which corresponded with at least some of these attributes in their preferred microhabitats (Price and Waser 1985). These seed and soil attributes therefore provide logical choices for characteristics likely to affect seed fate through heteromyid foraging activities.

In this paper I present evidence from laboratory foraging experiments that seed and soil attributes can affect seed harvesting and caching by three heteromyid species occurring in coastal sage scrub/grassland communities of southern California. These species are the San Diego pocket mouse (_Perognathus fallax_), the pacific kangaroo rat (_Dipodomys agilis_), and the Stephens kangaroo rat (_D. stephensi_)—a threatened species endemic to Riverside and San Diego Counties. I report results of a seed species preference experiment on the two kangaroo rat species using seeds of plant species occurring in their native habitats. I also report results of a patch choice experiment using commercial seeds in which artificial seed patches differing in soil properties and seed distribution patterns were

made available to individuals of all three rodent species. Finally, I discuss general implications of preferences and caching patterns revealed from these experiments for the fate of seeds in nature.

MATERIALS AND METHODS

Native Seed Choice Experiment

Mature seeds of four plant species occurring around Riverside, CA were collected in spring of 1985 and 1986. Two of the plant species are perennials: _Encelia farinosa_ Gray is a perennial shrub, and _Phacelia ramosissima_ Dougl. ex Lehm. is a perennial herb. The other two are annuals: _Erodium cicutarium_ (L.) L'Her. is a small introduced forb, widely distributed in deserts and mediterranean regions; _Avena barbata_ Brot. is an introduced grass which is virtually ubiquitous in southern California. For each of these plants mean unhusked seed weight was determined by weighing to the nearest 0.01 mg five replicate samples each consisting of 10 randomly selected seeds.

Four _D. agilis_ and seven _D. stephensi_ individuals were livetrapped around the Riverside area for use in preference experiments. The animals were housed individually at the University of California, Riverside, maintained on a 14:10 h light:dark cycle, and fed wild bird seed mix, lettuce, lab chow blocks, and mealworms. These animals were allowed to adjust to laboratory conditions for ≥ 5 months before experiments were initiated in November 1985. I conducted these experiments through August 1986, testing each individual kangaroo rat's preferences in four replicate trials. An additional animal of each species was available for replicates 3 and 4. I isolated animals in clean plexiglass cages 24 h prior to trials. These cages contained only the experimental animal, a "security" tin can, 2 cm of sand substrate, and an 8.5 cm diameter petri dish containing very fine sand (particles <0.25 mm) and 10 seeds of each of the above plant species. This amount of food was insufficient for 24 h maintenance need of animals. Thus, animals were deprived and therefore motivated to forage during trials, but had prior experience with the experimental seeds. The very fine sand mixed with seeds enabled animals to handle even the smallest seeds (i.e., _Phacelia_).

A trial consisted of presenting experimental animals with each of six possible pairwise combinations of the four seed species. Ten seeds of a given species were mixed with very fine sand in a 6.0 cm diameter plastic petri dish. Two such dishes containing different seed species set adjacent to each other at one end of the cage constituted a pairwise choice. A dim light approximating the intensity of full moonlight was cast on the cage to facilitate observation. I placed the first pairwise choice of seeds in an animal's cage and removed the security can.

Animals generally foraged immediately, and I left the petri dishes in the cage for as long as an animal foraged continuously. When foraging was interrupted by another activity I removed the first pairwise choice of seeds and replaced it with the second set of petri dishes containing seeds. This was repeated until all six pairwise seed combinations had been presented to and sampled by an animal. I noted which seed (i.e., petri dish) was chosen first from each pair. The order of presentation of the pairwise seed choices was randomly determined prior to each trial. The left/right position of seeds in each pairwise choice was alternated between consecutive trials. The duration of trials ranged from approximately 6 to 31 min.

Following trials I sieved the contents of each petri dish through a 0.85 mm wire mesh which retained seeds, but not sand. I counted the number of remaining seeds to determine numbers eaten by kangaroo rats. I also sieved all sand used as substrate in the arena to check for cached or spilled seeds.

I used two criteria--first seed dish chosen and majority taken from each pairwise choice--as indices of seed choice. Using each of these choice indices separately, I performed the following two analyses to test for seed species preferences in each kangaroo rat species. Both analyses use nonparametric statistics, because the replication of trials with the same individual animals invalidated the use of parametric techniques, which assume independence of observations.

First, I tallied the number of individual animals that selected a given seed type over the other in pairwise choices, and used a binomial test (Siegel 1956) to determine the probability of obtaining the observed outcome under the null hypothesis of random selection of seeds. When using majority taken as the seed choice index, I omitted all cases where an equal number of seeds were taken from the two petri dishes. Binomial test probabilities, determined separately for each replicate set of trials, were then combined across replicates (Sokal and Rohlf 1981, p. 779) to assess the overall probability of obtaining the observed outcome. This allowed me to determine whether the kangaroo rat species exhibited preferences, and whether preferences were transitive. A transitive preference ranking of four seed species requires that if A>B, B>C, and C>D, then A>C, A>D, and B>D, where A, B, C, and D are seed species and ">" means "preferred over." An example of intransitivity is A>B, B>C, C>D, but D>A.

Second, I scored the number of "wins" of each seed species in each trial (i.e., the number of times out of the six pairwise choices that an animal selected a particular seed species over the alternate seed). For this analysis, when using majority of seeds taken as the seed choice index, each seed species in a pairwise choice was given one-half of a win if equal numbers were taken. I ranked the number of wins of the four

seed species for each individual kangaroo rat, and used a Friedman's two-way ANOVA by ranks (Siegel 1956) to test for concordance of preference patterns among individuals in each replicate trial. I then combined the probabilities associated with these Friedman's tests across replicate trials (Sokal and Rohlf 1981, p. 779) to obtain an overall test of concordance among animals of each species. Similarly, I tested for concordance of preference patterns within each individual kangaroo rat across replicates. Finally, I tested for concordance of preference patterns between D. stephensi and D. agilis.

Seed Patch Choice Experiment

In this experiment five Dipodomys agilis and D. stephensi individuals from the above experiment and five P. fallax individuals livetrapped in the Riverside area were allowed to forage in a large (3 X 6 m) indoor arena at the University of California, Riverside. Care of the animals was as described for the previous experiment. The following protocol has been described in greater detail by Price and Waser (1985).

The floor of the foraging arena was composed of a grid of 20 X 20 cm tiles with an even layer of purified sand glued to the exposed surface for traction. These tiles could be removed and replaced by equal size wooden frames with screen bottoms. In the frames I constructed eight different artificial seed patch types consisting of all possible combinations of two soil densities (vermiculite = 0.2 g/cm^3 or sand/gravel = 1.5 g/cm^3), two soil textures (fine particles = 0.85-1.2 mm or coarse particles = 2.8-4.75 mm), and two seed dispersion patterns (100 millet seeds placed in two equal-sized clumps or evenly scattered). I placed the seeds between two 1 cm layers of substrate. One of each patch type was substituted for a tile at each of three distances from a nest box which opened into a corner of the arena. Patch locations were randomly determined under the constraint that none was placed <40 cm from the arena walls or <20 cm from another patch. Purified sand was then spread evenly over the floor of the arena except for the seed patches.

The foraging arena room was on a 14:10 h light:dark cycle corresponding to the cycle of the animal housing facility. I placed a single animal in the arena's nest box during the last hour of light and allowed it to forage for the 10 h dark period. Animals remained in the nest box and did not forage until lights went off. Shortly after lights came back on I removed the experimental animal and counted any seeds cached in the nest box. I sieved each seed patch to determine numbers of seeds removed, and noted obvious cases of caching (scatterhoarding) in seed patches (i.e., when >100 seeds were in a patch). I assumed that no seeds were removed from a patch that had been used as a caching site. I then vacuumed all sand from the arena and sieved it for cached seeds.

The three heteromyid species were rotated through experimental trials until all five animals of each species had been used. No animal had prior experience with the foraging arena, and none was used more than once.

I used the number of seeds taken from each patch as a dependent variable and the eight patch types as independent variables in a separate ANOVA for each animal to test for individual patch preferences. These ANOVA's included planned comparisons for each of the seed and soil features defining patch types (i.e., clumped vs scattered seeds, heavy vs light soil, large vs small soil particles). I also analyzed the seed consumption data on a per species basis by summing the number of seeds taken by each animal from the three representatives of each patch type, and expressing these values as relative proportions of total seeds taken by the individual during one night's foraging. After normalizing by arcsine transformation, I used these relative consumption values as dependent variables and rodent species, seed dispersion, and soil density and texture as independent variables in a four-way ANOVA. This analysis was used only in an illustrative manner to check which variables might influence patch preferences. The use of relative proportions, which are obviously interrelated, violates the assumption of independence implicit to ANOVA. Therefore, probability levels from this analysis are too high. I chose to use relative rather than absolute seed consumption because different rodent species and individuals took substantially different numbers of seeds.

Normalized mean seed consumption values from each of the eight patch types were also used as dependent variables in MANOVA's with the three rodent species as independent variables to test for interspecific differences in patch choice. Duncan's multiple range tests revealed which species differed significantly.

RESULTS

Native Seed Choice Experiment

Seeds of the four plant species offered to kangaroo rats differed in weight by orders of magnitude (Table 1). The smallest seed (Phacelia) falls just above the reported minimum seed weight utilized by desert heteromyids--0.25 mg (Price and Reichman 1987). Thus, one might expect heteromyids to discriminate against Phacelia seeds in choice experiments.

Dipodomys stephensi and D. agilis individuals exhibited transitive preference patterns in 93% and 61% of seed choice trials, respectively. Phacelia was consistently the least preferred seed in these trials. From numbers of D. stephensi individuals choosing particular seed types in pairwise choices, and binomial test probabilities associated with these ratios (Table 2)[1], the following transitive seed ranking scheme can be readily deduced:

Table 1. Mean unhusked seed weights (mg) of four plant species used in seed choice experiment. N = 50 seeds/plant species.

Seed type	Weight/seed ± SD (mg)
Avena barbata	38.95 ± 3.30
Erodium cicutarium	2.62 ± 0.17
Encelia farinosa	0.50 ± 0.08
Phacelia ramosissima	0.26 ± 0.03

Avena = Erodium > Encelia > Phacelia,

where "=" indicates equal ranking and ">" means "preferred over." D. stephensi shows this pattern regardless of whether first seed chosen or majority of seeds taken is used as the choice index. Choice ratios for D. agilis are suggestive of the same ranking pattern, but the smaller number of individuals tested precludes statistical support for preference in some cases (Table 2). It is interesting, however, that Phacelia is included in nearly every pairwise choice in which D. agilis expresses a significant preference, and the alternate seed is always preferred over Phacelia.

For both of the seed choice indices there was significant concordance (P < 0.05) in seed ranking patterns among D. agilis individuals in two of the four sets of replicate trials. Combining probabilities across trials indicates overall concordance in ranking among individuals for first seeds chosen (X^2 = 19.19, df = 8, P < 0.025) and for majority of seeds taken (X^2 = 29.14, df = 8, P < 0.001). Concordance among D. stephensi individuals was significant (P < 0.02) in all trials based on majority of seeds taken (combined probabilities: X^2 = 50.29, df = 8, P < 0.001), and in three of four trials based on first seeds chosen (combined probabilities: X^2 = 33.17, df = 8, P < 0.001). Individual animals were generally concordant across trials in their seed ranking patterns. Six out of eight D. stephensi and three of five D. agilis individuals were significantly concordant (P < 0.05) across replicates based on first seeds chosen. Five D. stephensi and two D. agilis individuals showed significant concordance (P < 0.05) across replicates based on majority of seeds taken.

Concordance between ranking patterns of the two kangaroo rat species was also significant (Table 3), based on either seed choice criterion (first seeds chosen: X_r^2 = 19.16, df = 3, P < 0.001; majority of seeds taken: X_r^2 = 22.54, df = 3, P < 0.001).

[1] Table 2 gives numbers of individuals choosing each seed type in all replicate sets of trials combined. Detailed data on a per replicate basis will be given in Longland and Price (in prep.).

Table 2. Seed choice by _Dipodomys agilis_ and _D. stephensi_. Values are numbers of animals choosing each seed type in pairwise seed choices pooled across four replicate trials per individual. Choice is based on (A) first seed chosen, and (B) majority of seeds taken. Seed types are listed in Table 1, and are abbreviated by the first two letters of the genus. Binomial test probabilities associated with the outcome of each replicate were calculated under the assumption of random seed selection. These probabilities were combined across replicates to give an overall significance level for each pairwise choice (*: P < 0.05, **: P < 0.01, ***: P < 0.001, NS: P > 0.10).

Rodent species	A. Choice index: first seed chosen Pairwise seed choices						B. Choice index: majority of seeds taken Pairwise seed choices					
	Av:Er	Av:En	Av:Ph	Er:En	Er:Ph	En:Ph	Av:Er	Av:En	Av:Ph	Er:En	Er:Ph	En:Ph
Dipodomys agilis	11:7 NS	13:5 NS	14:4 NS	13:5 NS	16:2 *	16:2 ■	5:6 NS	11:5 NS	14:3 ■	14:1 ■	17:0 ■■	15:2 ■
Dipodomys stephensi	13:17 NS	26:4 ***	29:1 ■■■	28:2 ***	29:1 ***	26:4 ■■	7:14 NS	19:5 ■■	27:1 ***	19:0 ***	29:0 ■■■	26:1 ■■■

The transitive and concordant seed ranking patterns demonstrated here have important implications. Transitivity suggests that seed preferences are based on a single criterion, such as seed size, and not on ■ combination of potentially conflicting criteria. Concordance within and among individuals of each species suggests that the basis for seed preference does not change. Concordance between species suggests that the similar preferences exhibited by the two kangaroo rat species are based on the same criterion.

Seed Patch Choice Experiment

ANOVA's indicate that most (13 of 15) individuals of all three heteromyid species expressed significant preferences for certain seed patches or patch characteristics among the eight patch types (Table 4). Planned comparisons for features defining patch types revealed that all five _Dipodomys agilis_ and _D. stephensi_ individuals preferred clumped-seed patches over those with scattered seeds. Three _Perognathus fallax_ individuals showed the same preference. Nobody preferred scattered seeds. Differences between the rodent species in individual patch preferences occurred mainly with respect to soil density differences.

Table 3. Number of "wins" (i.e., pairwise choices in which a given seed species was chosen over the alternate seed) of seed species presented to _Dipodomys agilis_ and _D. stephensi_ in four replicates of seed choice experiment. Choice is based on (A) first seed chosen, and (B) majority of seeds taken. There is significant concordance between preference patterns expressed by the two rodent species using either choice criterion (*: P < 0.001).

Rodent species	Rep	A. Choice criterion: first seed chosen* Seed species (# "wins")				B. Choice criterion: majority of seeds taken* Seed species (# "wins")			
		Avena	Erodium	Encelia	Phacelia	Avena	Erodium	Encelia	Phacelia
Dipodomys agilis	1	10	8	6	0	17	16	8.5	0.5
	2	11	5	6	2	14	18	8.5	1
	3	10	11	5	4	16	19.5	11	1.5
	4	8	12	8	2	15	18	14	1
Dipodomys stephensi	1	18	17	7	0	7	12	5	0
	2	14	18	6	4	8.5	8.5	6	1
	3	17	21	9	1	9.5	10	7.5	4
	4	19	19	9	1	11	12	6.5	0.5

Table 4. Number of <u>Dipodomys</u> <u>agilis</u> (DA), <u>D.</u> <u>stephensi</u> (DS), and <u>Perognathus</u> <u>fallax</u> (PF) individuals exhibiting significant (P < 0.05) preferences among eight seed patch types and three dichotomous characteristics defining patch types. N = 5 individuals for all species.

Basis of patch discrimination	Patch characteristics	Number of animals exhibiting preferences		
		DA	DS	PF
Patch-type		4	4	3
Seed dispersion	clumped	5	5	3
	scattered	--	--	--
Soil texture	coarse	--	--	--
	fine	--	--	1
Soil density	heavy	--	2	--
	light	1	--	2

Table 5. Distribution of seed caching in eight seed patch types by <u>Dipodomys</u> <u>agilis</u> (DA), <u>D.</u> <u>stephensi</u> (DS), and <u>Perognathus</u> <u>fallax</u> (PF). Values are total numbers of patches used for seed caching by five animals per species.

Patch type			Rodent species		
Seed dispersion	Soil texture	Soil density	DA	DS[1]	PF
Clumped	coarse	heavy	--	--	4
		light	--	--	2
	fine	heavy	--	--	2
		light	--	1	--
Scattered	coarse	heavy	2	1	2
		light	--	5	1
	fine	heavy	2	1	--
		light	--	1	2

[1] Significantly different than random multinomial distribution (P < 0.01).

Four-way ANOVA supports the results of the ANOVA's for individual animals: the only highly significant factors accounting for seed consumption differences between patch types are "seed distribution" (F = 97.91, df = 1,96, P < 0.0001) and the "rodent species X soil density" interaction (F = 8.51, df = 1,96, P < 0.0004). This indicates that a seed distribution preference shared by all species, and soil density preferences which differ between species are the strongest determinants of patch preferences.

The higher proportions of seeds harvested from clumped as opposed to scattered seed patches were striking for all of the rodent species[1]. MANOVA results indicate that relative patch use differed between the species for three of the eight patch types: (1) patches with clumped seeds and fine, heavy soil (CFH); (2) clumped-seed patches with fine, light soil (CFL); and (3) scattered-seed patches with fine, light soil (SFL). <u>P. fallax</u> took a significantly lower proportion of seeds from CFH patches than <u>D. stephensi</u> (F = 4.74, df = 2,12, P < 0.04), and more seeds from CFL patches than either kangaroo rat species (F = 6.99, df = 2,12, P < 0.01). <u>D. stephensi</u> took fewer seeds from SFL patches than the other two species (F = 8.78, df = 2,12, P < 0.005).

Seed caching was generally concentrated in scattered-seed patches (Table 5). <u>P. fallax</u> and <u>D. agilis</u> caching patterns were not significantly different from a random multinomial caching distribution (P > 0.05). However, <u>D. stephensi</u>

cached nonrandomly (P = 0.0015). Five of nine caches by this species were in scattered-seed patches with coarse, light soil (Table 5). Because the patches contained seeds before animals cached in them, and some of these may have been removed before caching, it would be fruitless to attempt to determine numbers deposited by animals. However, numbers of seeds cached in the nest box and in the foraging arena outside of patches can be determined. These numbers were so variable between individuals of the heteromyid species that they are of limited use (Table 6). However, a noteworthy point is that <u>D. stephensi</u> scatterhoarded very few seeds in the arena compared to the nest box, or compared to scatterhoards of other species.

Table 6. Seed caching in nest box and in scatterhoards (within foraging arena, but not in seed patches) by <u>Dipodomys</u> <u>agilis</u> (DA), <u>D. stephensi</u> (DS), and <u>Perognathus</u> <u>fallax</u> (PF). Values are mean number of seeds cached per animal (±SD) averaged over five animals per species. Values in parentheses are ranges of numbers of seeds cached per animal.

Number of seeds	Rodent species		
	DA	DS	PF
Scatterhoards	236.8±461.8 (4-1059)	11.0±4.8 (3-16)	208.0±212.1 (3-436)
Nest box	295.8±202.2 (120-645)	268.6±308.8 (0-685)	166.8±192.1 (0-460)

[1] Proportions of seeds harvested from each patch type will be given in Longland and Price (in prep.).

DISCUSSION

The heteromyid species studied here exhibited seed and soil preferences in their foraging activities. The question of primary importance now is: How can these preferences affect seed pools or the fate of seeds in range plant populations?

Implications of the seed species preference experiments with Dipodomys agilis and D. stephensi are straightforward. Plant species whose seeds are highly preferred, such as Avena and Erodium, should experience relatively higher rates of seed predation and dispersal from these kangaroo rats than plants with low ranking seeds. Of course, absolute rates of seed predation and caching will also depend on factors which must be measured in the field, such as numbers of seeds set by plants, local rodent and plant population densities, and temporal seed set patterns.

There is evidence that heteromyids generally prefer large seeds over small ones (Reichman 1975, 1979, Price 1983). The seed species ranking pattern exhibited by D. stephensi, and to a lesser extent by D. agilis (Table 2), seems to be a direct function of seed size (Table 1). Thus, the transitivity in ranking demonstrated above may well be based on relative seed sizes. The only anomaly here is that Avena and Erodium were equally preferred, and seeds of the former are more than an order of magnitude larger than those of the latter. From the perspective of optimal foraging theory one would expect a preference for Avena seeds because of the apparent profitability of such a large seed. It is unlikely that these seeds are too difficult for kangaroo rats to handle. They manipulate Avena and similarly-sized seeds, such as sunflower, adroitly in captivity. Perhaps Avena seeds contain secondary compounds which limit consumption, or Erodium seeds afford some nutritional benefit lacking in Avena. It is also certainly possible that the correlation between seed size and ranking is fortuitous. A robust test for seed size preferences should offer seeds of different sizes, but uniform quality (e.g., one kind of seed ground and sieved to different size fractions).

If kangaroo rat seed preferences are truly size-dependent, the implications of this experiment extend beyond the four plant species whose seeds were used. In this case, large-seeded plant species would generally experience the highest rates of seed predation and dispersal from these rodents. Seed size preferences could also have profound effects on recruitment of plant species having seed size polymorphisms. For example, Indian rice grass (Oryzopsis hymenoides [R. & S.] Ricker.) has polymorphic seeds with different germinabilities, and kangaroo rats preferentially harvest and cache the largest, most germinable seeds (McAdoo et al. 1983).

Heteromyids tend to prefer high density seed patches in their foraging activities (Reichman 1979, 1983, Price and Waser 1985). In patch choice experiments all three heteromyid species clearly preferred clumped over scattered-seed patches, although this preference was less pronounced for Perognathus fallax than for the two kangaroo rats (Tables 4 and 5). Such preferences probably result from high profitability and/or conspicuousness of seed aggregations, and suggest that the probability of a seed being harvested may be a function of its proximity to neighboring seeds. For example, Evans et al. (1983) found that singly-planted bitterbrush (Purshia tridentata [Pursh] DC.) seeds were not harvested by rodents, but aggregations of two or more seeds usually were. If this is a general phenomenon, plants with temporally restricted seeding phenologies should experience higher levels of seed predation and dispersal than plants with longer seeding phenologies, because seeds of the former should be more temporally and spatially aggregated.

While the three heteromyid species showed little tendency for selection of seed patches on the basis of soil texture, they did display different preferences for patches based on soil density (Table 4). P. fallax, which frequents rocky and shrub-covered microhabitats (Price and Waser 1984), preferred patches with light soil. D. stephensi occurs in large open habitats (annual grasslands), and preferred heavy soil patches. D. agilis, a specialist on open microhabitats between shrubs (Price and Waser 1984), was less discriminating in regard to soil density. Open microhabitats in the desert are typified by heavier soils than shrub microhabitats (Price and Reichman 1987). If this relationship between microsite and substrate density holds for coastal sage scrub habitats in southern California, which are similar to deserts in many ways, then the soil density preferences exhibited by these heteromyids correspond qualitatively to edaphic conditions in their preferred habitats and microhabitats. This, in turn, means that the probability of seeds being harvested should be sensitive to their distributions among microhabitats, to the local species composition of rodents, and to relative densities of different rodent species.

The patch choice results provide less information about determinants of seed caching. A similar experiment in which various seed-free patches differing in edaphic conditions are made available to rodents for caching seeds from some outside source would be more revealing. However, the data do suggest that the heteromyid species are more likely to cache in areas where seed distributions are scattered than around pre-existing clumps of seeds (Table 5). It also appears that D. stephensi preferred certain soil types as caching sites. If edaphic conditions which favor germination and establishment of a plant species happen to correspond with conditions in preferred caching sites of locally abundant rodent species then heteromyid caching behavior could benefit the plant species. The extent to which such a plant species is benefitted by caching will depend on relative numbers of seeds cached vs consumed, and the probability of cache recovery for future consumption. While quantifying such parameters is not a trivial task, it is nevertheless feasible.

Overall, these experiments suggest that probabilities of seed harvest and/or caching by heteromyid rodents are complex functions of several variables including seed species, seed sizes and distributions, edaphic conditions, rodent microhabitat affinities, and local rodent species composition. Obviously, local densities of seeds and rodents should also be important. Heteromyids utilize large quantities of seeds, and they gather and disperse (cache) these seeds in a nonrandom manner. Consequently, plant distributions and abundances may result at least partially from rodent foraging activities, rather than simply being the result of environmental requirements for germination and establishment.

ACKNOWLEDGMENTS

LITERATURE CITED

Batzli, George O. and Frank A. Pitelka. 1970. Influence of meadow mouse populations on California grasslands. Ecology 51:1027-1039.

Borchert, M. I. and S. K. Jain. 1978. The effect of rodent seed predation on four species of California annual grasses. Oecologia 33:101-113.

Bowers, Michael A. 1982. Foraging behavior of heteromyid rodents: field evidence of resource partitioning. J. Mammal. 63:361-367.

Brown, James H. and Diane W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science 196:880-882.

Brown, James H. and Gerald A. Lieberman. 1973. Resource utilization and coexistence of seed-eating rodents in sand dune habitats. Ecology 54:788-797.

Brown, James H., O. J. Reichman, and Diane W. Davidson. 1979. Granivory in desert ecosystems. Ann. Rev. Ecol. Syst. 10:201-227.

Chew, Robert M. and Alice E. Chew. 1970. Energy relationships of mammals of a desert shrub (Larrea tridentata) community. Ecol. Monogr. 40:1-21.

Davidson, Diane W., James H. Brown, and Richard S. Inouye. 1980. Competition and the structure of granivore communities. Bioscience 30:233-238.

Evans, Raymond A., James A. Young, Greg J. Cluff, and J. Kent McAdoo. 1983. Dynamics of antelope bitterbrush seed caches. USDA For. Ser. Gen. Tech. Rep. INT-152:195-202.

Harris, John H. 1984. An analysis of desert rodent foraging ecology. Ecology 65:1579-1584.

Harris, John H. 1986. Microhabitat segregation in two desert rodent species: the relation of prey availability to diet. Oecologia 68:417-421.

LaTourrette, Joseph E., James A. Young, and Raymond A. Evans. 1971. Seed dispersal in relation to rodent activities in seral big sagebrush communities. J. Range Manage. 24:118-120.

McAdoo, J. Kent, Carol C. Evans, Bruce A. Roundy, James A. Young, and Raymond A. Evans. 1983. Influence of heteromyid rodents on Oryzopsis hymenoides germination. J. Range Manage. 36:61-64.

Nelson, James F. and Robert M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. Am. Midl. Nat. 97:300-320.

Price, Mary V. 1978. The role of microhabitat in structuring desert rodent communities. Ecology 59:910-921.

Price, Mary V. 1983. Laboratory studies of seed size and species selection by heteromyid rodents. Oecologia 60:259-263.

Price, Mary V. and Stephen H. Jenkins. 1987. Rodents as seed consumers and dispersers. Chpt. 5 in Seed Dispersal, David R. Murray (ed.), Academic Press, Australia.

Price, Mary V. and O. J. Reichman. 1987. Spatial and temporal heterogeneity in Sonoran Desert seed pools, and implications for heteromyid rodent foraging. Ecology 68:in press.

Price, Mary V. and Nickolas M. Waser. 1984. On the relative abundance of species: postfire changes in a coastal sage scrub community. Ecology 65:1161-1169.

Price, Mary V. and Nickolas M. Waser. 1985. Microhabitat use by heteromyid rodents: effects of artificial seed patches. Ecology 66:211-219.

Pulliam, H. Ronald and Marina R. Brand. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology 56:1158-1166.

Reichman, O. J. 1975. Relationships of desert rodent diets to available resources. J. Mammal. 56:731-751.

Reichman, O. J. 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology 60:1085-1092.

Reichman, O. J. 1983. Behavior of desert heteromyids. Great Basin Nat. Memoirs 7:77-90.

Reynolds, Hudson G. 1950. Relation of Merriam
    kangaroo rats to range vegetation in southern
    Arizona. Ecology 31:456-463.

Reynolds, Hudson G. and G. E. Glendening. 1949.
    Merriam kangaroo rat, a factor in mesquite
    propagation on southern Arizona rangelands. J.
    Range Manage. 2:193-197.

Rissing, Steven W. 1981. Foraging specializations
    of individual seed-harvester ants. Behav.
    Ecol. Sociobiol. 9:149-152.

Rissing, Steven W. 1986. Indirect effects of
    granivory by harvester ants: plant species
    composition and reproductive increase near ant
    nests. Oecologia 68:231-234.

Rosenzweig, Michael L. and Jerald Winakur. 1969.
    Population ecology of desert rodent
    communities: habitats and environmental
    complexity. Ecology 50:558-572.

Siegel, Sidney. 1956. Nonparametric statistics
    for the behavioral sciences. McGraw-Hill, New
    York.

Sokal, Robert R. and F. James Rohlf. 1981.
    Biometry. Freeman and Co., San Francisco.

Tomback, Diana F. 1982. Dispersal of whitebark
    pine seeds by Clark's nutcracker: a mutualism
    hypothesis. J. Animal Ecol. 51:451-467.

Vander Wall, Stephen B. and Russell P. Balda.
    1977. Co-adaptations of the Clark's nutcracker
    and the piñon pine for efficient seed harvest
    and dispersal. Ecol. Monogr. 47:89-111.

SELECTION PROCEDURES FOR IMPROVING SEEDLING ESTABLISHMENT IN COOL-SEASON RANGE GRASSES

Douglas A. Johnson and Kay H. Asay[1]

ABSTRACT

Screening procedures to identify breeding lines that exhibit superior establishment are essential in the improvement of cool-season forage grasses for semiarid rangelands. Both seed weight and emergence from a deep planting depth have been used to produce improved cultivars of Russian wildrye and crested wheatgrass. Other potential screening techniques include the combination of a line-source sprinkler system and a rainout shelter facility, and evaluation of the stable carbon isotopic composition of breeding lines.

INTRODUCTION

Cool-season range species are seeded for a variety of reasons (Stoddart et al. 1975) including: revegetation of abandoned croplands, vegetation replacement following fire, expansion of the grazing season, improvement of the quantity and quality of forage, reestablishment of native forage plants, and erosion protection. Regardless of the objective, the seedling establishment stage is extremely critical. Frequently, establishment success determines the performance of the plant in the rangeland environment. The potential for stand failure is a major consideration in seeding rangelands. Given the cost of seedings, stand failure represents a major financial risk. Selecting plant materials with superior establishment characteristics will increase the success of rangeland seedings.

Although many environmental factors influence the growth and production of cool-season range plants on arid and semiarid rangelands, drought is probably the most important factor (Johnson 1986b). Drought can occur sporadically during seedling establishment and may interrupt germination and seedling development. Drought is particularly critical during establishment because seedlings have not developed extensive root systems that allow them to tap water and nutrient supplies nor have they accumulated carbon products necessary for respiratory maintenance during long drought-induced dormancy periods. As a result, a seedling is limited in its ability to either tolerate or avoid drought.

The U. S. Department of Agriculture's Agricultural Research Service (USDA-ARS) in cooperation with

Utah State University has assembled a multidisciplinary research team at Logan, Utah, to develop improved grasses, legumes, and forbs for use on rangelands of the Intermountain Region of the western U.S. This team consists of cytogeneticists, breeders, plant physiologists, range scientists, and a nematologist. The team uses hybridization, breeding, and selection to provide a broad spectrum of improved plants for conservation, reclamation, recreation, and production. Just as farmers in the western U.S. would not use crop varieties developed for the midwestern or southeastern U.S., range managers in the arid and semiarid West should not have to rely on forages bred and selected for use in more mesic areas. Only by using adapted forages that can successfully establish and survive in the rigorous rangeland environment will returns from range seedings be optimized.

IMPORTANCE OF PLANT SELECTION PROCEDURES

Progress in any plant improvement program depends on the amount of heritable genetic variation for the characteristic(s) in question. A broad genetic base of germplasm must be assembled to maximize the genetic diversity available for selection. A broad germplasm base increases the probability of obtaining desirable genetic variation. However, a broad germplasm base necessitates screening large populations to find plants that exhibit the desired characteristics.

Screening procedures to identify forage breeding lines that exhibit superior establishment are discussed by Johnson (1980, 1986a) and Johnson et al. (1981). Ideally these techniques should: 1) assess plant performance at the critical development stage, 2) be completed in a relatively short time, 3) use small quantities of plant material and be nondestructive, and 4) be capable of screening large breeding populations. Field evaluation in droughty rangeland environments is generally regarded as the standard for assessing range forage species. However, because precipitation varies greatly among sites and years in arid and semiarid environments, effective field selection for seedling establishment involves testing on many rangeland sites scattered over a wide geographical area. These field evaluations are difficult, particularly early in selection when seed quantities of breeding lines are extremely limited. Additionally, these procedures are time-consuming and expensive. Consequently, a combination of field and laboratory screening procedures is most effective in selecting forage breeding lines that establish well under water-limited conditions.

Numerous plant characteristics are known to affect production and survival under drought. These characteristics are classically categorized into avoidance and tolerance mechanisms (Levitt 1972). Avoidance mechanisms allow the plant to escape drought, whereas tolerance mechanisms enable the plant to postpone or withstand dehydration. Avoidance and tolerance adaptations include a wide variety of morphological and physiological mechanisms. A more thorough discussion of these

---

various characteristics as they relate to range forage species is presented by Johnson et al. (1981).

Because of the many interactions between morphological and physiological characteristics and drought, Wright (1971) stated that no single plant characteristic reliably indicates drought resistance in range plants. Ashton's (1948) statement concerning drought selection is still applicable today: "In general, physical characters such as water requirements and transpiration rate, and anatomical characters have not been found to provide a simple and practical index of drought resistance in selection work." Consequently, Wright (1964) recommended that until more was known about the characteristics of drought resistance, plant improvement programs should rely on whole-plant response to drought rather than on specific plant characteristics.

FIELD-LABORATORY SCREENING COMPARISONS

Asay and Johnson (1980, 1983) compared the results of various laboratory screening procedures with field establishment trials for Russian wildrye [Psathyrostachys juncea (Fisch.) Nevski] and crested wheatgrass [Agropyron cristatum (L.) Gaertn. and A. desertorum (Fisch. ex Link) Schult.]. We hoped to identify seedling responses that could be evaluated in the laboratory to select breeding lines with superior establishment potential. The seedling responses evaluated for crested wheatgrass included seedling emergence under controlled drought, seedling recovery after exposure to drought, and seed weight. Russian wildrye seedlings were evaluated for their ability to emerge from a deep planting depth as well as for the other three traits. The techniques used in screening for these seedling responses will be described briefly.

Seedling Emergence Under Controlled Drought

The ability of seedlings to emerge under controlled drought was determined in the laboratory using the technique of Johnson and Asay (1978). Soil in germination vessels was separated from a polyethylene glycol-6000 (PEG-6000) osmotic solution with a cellulose acetate membrane. The pore size of the membrane and the large molecular weight PEG-6000 were matched so that water could move across the membrane, but the PEG-6000 could not. By adjusting the concentration of the PEG-6000 solution, the matric potential of the soil could be controlled. Because the technique avoids any direct contact between the seed and osmoticum, confounding of results by specific effects of the osmotic solution on the seed are minimized. Soil water potentials of -0.58 and -0.84 MPa were used for the 134 progenies of Russian wildrye (Asay and Johnson 1980), whereas soil water potentials for the 170 crested wheatgrass progenies were -0.35 and -0.55 MPa (Asay and Johnson 1983). After the soil equilibrated at the desired water potential, 25 seeds of each progeny were uniformly distributed over the soil surface and covered with about 0.5 cm of air-dried soil. Plastic containers, each containing two germination vessels, were then sealed and placed in a controlled-temperature incubator at 25 C with no light. Trials were replicated three or four times, and seedlings were counted after 7 to 11 days.

Seedling Recovery After Drought Exposure

The laboratory procedures used to screen the progenies of crested wheatgrass and Russian wildrye were similar to those described by Wright (1964). Cone-shaped plastic containers whose diameter of 3.8 cm at the top tapered over the 21 cm length to 2.5 cm at the bottom were used. Three seedlings were transplanted in each plastic container. After 3 weeks in the greenhouse, the plants were transferred to a growth chamber programmed to provide a 12-h daylength, 30/10 C day/night temperatures, 20/60% day/night relative humidity, and 900 uE/m^2/sec quantum flux density between 400 and 700 nm. In general, experimental units (which consisted of seven containers for each entry) were arranged as a randomized complete block with three or four replications. After a 1-week period for the plants to equilibrate to growth chamber conditions, water was withheld from the plants for 17 days. The desiccated plants were then returned to the greenhouse and watered daily for 3 weeks. Three independent observers rated each group of 7 containers for degree of recovery on a scale of 1 to 9 (1 = no living plants and 9 = maximum recovery based on number of living tillers and green leaf area).

Seedling Emergence From Deep Planting Depth

Seedlings of the 134 progenies of Russian wildrye were also evaluated for their ability to emerge from a seeding depth of 7.6 cm. Fifty seeds of each progeny line were planted in rows 14.5 cm long and 5 cm apart in stainless steel flats that were 57 cm long, 43 cm wide, and 11 cm deep. The flats were then placed in a growth chamber that was programmed as described above for the seedling recovery trials. The experimental design was a randomized complete block with four replications. Water was applied on alternate days to maintain uniform soil-moisture conditions. The number of emerged seedlings were counted 10 days after planting.

Field Establishment Trials

Stand establishment in the field was evaluated for the same crested wheatgrass and Russian wildrye progenies included in the laboratory trials. The crested wheatgrass progenies were evaluated at two sites, one located near Park Valley, Utah, and the other near Malta, Idaho; the sites received about 245 and 285 mm annual precipitation, respectively. The Russian wildrye progenies were assessed only at the site near Park Valley, Utah. Plots were sown during early November, and seeds did not germinate until the following spring. Each plot consisted of a 3-m row in which 500 seeds were planted in soil at 3.5 cm with a cone seeder

Table 1. Simple correlation coefficients (r) between laboratory and actual field establishment characteristics in crested wheatgrass and Russian wildrye (from Asay and Johnson 1980, 1983).

Field Criteria	Seed Weight	7.6 cm planting Emerg.	7.6 cm planting Dry Wt.	Emerg. under drought [1] Mod. Stress	Emerg. under drought [1] High Stress	Seedling Recovery
		Laboratory Characteristics				
Crested Wheatgrass (n=120)						
Emergence (May)	0.48**	–	–	-0.02	-0.08	0.05
Dry Wt. (July)	0.49**	–	–	0.23*	0.12	0.15
% Stand (Oct.)	0.51**	–	–	-0.01	-0.04	0.22*
Russian Wildrye (n=134)						
Emergence (May)	0.15*	0.24**	0.23**	0.14	0.07	0.01
Dry Wt. (Aug.)	0.24**	0.33**	0.22**	0.00	-0.15	-0.09
% Stand (Oct.)	0.08	0.21*	0.18*	-0.05	0.01	-0.02

*,**Significant at 0.05 and 0.01 probability levels, respectively
[1]Moderate Stress = -0.35 MPa for crested wheatgrass and -0.58 MPa for Russian wildrye.
 High Stress = -0.55 MPa for crested wheatgrass and -0.84 MPa for Russian wildrye.

equipped with a double-disc furrow opener. Data were obtained from the center 1.8 m section of the plot. Plots were arranged as randomized complete blocks with 2 replications at the Malta site and 4 replications at Park Valley. Seedlings were counted during mid-May, seedling dry weight was obtained in July for crested wheatgrass and in August for Russian wildrye, and stand percentage was determined in October.

Laboratory-Field Correlations

In general, significant genetic variation was found for nearly every characteristic evaluated in the laboratory (Asay and Johnson 1980, 1983). For most characteristics genetic variance accounted for more than 50% of the phenotypic variance. Although the genotype X environment interaction was significant in some cases, the amount of genetic variation appeared ample for improvement by selection. However, improvement of these laboratory characteristics by selection would not necessarily improve seedling establishment under field conditions. Consequently, laboratory characteristics must be directly related to actual field establishment to identify the most meaningful laboratory characteristics.

The laboratory and field correlations (r) for the crested wheatgrass and Russian wildrye progenies are presented in Table 1. For crested wheatgrass, the most consistent correlation occurred with seed weight (0.48 to 0.51). Seed weight was also significantly and positively correlated with emergence and seedling dry weight in Russian wildrye, but to a lesser degree (0.15 and 0.24, respectively). The correlation between seed weight and percent stand was low (0.08) and not significant for Russian wildrye.

Except for emergence and dry weight of seedlings planted at a 7.6 cm planting depth, none of the other laboratory characteristics was significantly related to the field criteria in Russian wildrye. All correlation coefficients between the field criteria and emergence from a 7.6 cm planting depth were positive and statistically significant, and ranged from 0.18 to 0.33. These correlations were generally higher than those between seed weight and the field criteria, suggesting that seedling establishment in Russian wildrye probably would be improved more by selecting for emergence from a deep seeding depth than for seed weight. Unfortunately, ability to emerge from a deep depth was not evaluated for the crested wheatgrass progenies. Although higher correlations would be desirable, these probably are high enough for meaningful genetic progress.

Given the significant correlations between emergence and field performance, the ability of seedlings to emerge from a deep planting depth was used to select Russian wildrye for improved establishment. These evaluations together with field agronomic performance resulted in the release of the Russian wildrye cultivar Bozoisky-Select (Asay et al. 1985a). Similar procedures were used to develop the crested wheatgrass cultivar Hycrest (Asay et al. 1985b). Both Bozoisky-Select and Hycrest have shown marked improvement in seedling establishment under rangeland conditions. Ongoing selection is further improving the seedling establishment of Russian wildrye.

The ability to emerge from a deep planting depth is demonstrated in figure 1 for various Russian wildrye entries, including Vinall (a long-standing cultivar), Cabree (a cultivar selected for seed retention only), Bozoisky-Select (above), and Syn-A (recently developed population obtained using intensive selection for ability to emerge from a deep seeding depth). Fifty seeds of each
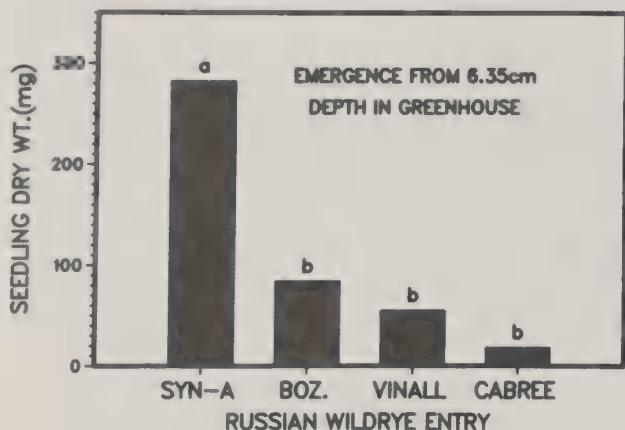
Figure 1. Seedling dry weight of four Russian
wildrye entries planted at a depth of
6.35 cm and grown in a greenhouse for
6 weeks.

entry with 6 replications in a randomized complete
block design were planted in stainless steel trays
at a seeding depth of 6.35 cm.   After 6 weeks,
seedling dry weight was determined.   Shoots of
Syn-A weighed more than three times as much as any
of the other Russian wildrye entries.   It was
followed by Bozoisky-Select, Vinall, and Cabree.
Actual field studies involving these entries also
showed that Syn-A has significantly better
establishment than presently available Russian
wildrye cultivars (Asay and Horton, unpublished).
Although some of this improvement can be
attributed to newly acquired germplasm, the
laboratory selection techniques certainly
contributed to this improved establishment.

OTHER PROMISING SCREENING PROCEDURES

Line-Source Sprinkler Systems

Line-source sprinkler systems were first described
by Hanks et al. (1976) and have been used widely
in studying the effects of water stress on crop
growth and evapotranspiration.   In this system,
sprinklers are spaced along an irrigation line
such that the water distribution pattern is
constant along any line parallel to the sprinkler
line.   Perpendicular from the sprinkler line, the
amount of water applied decreases gradually with
distance from the line.   As a result, the water
application pattern is uniform along the length of
the irrigation line and continuously but uniformly
variable at right angles to the sprinkler line.
Such a system is ideal for examining the response
of forage breeding lines to various water
applications, provided evaluations are conducted
in dry areas or during drought periods.

In addition to the typical field line-source
sprinkler system, Johnson et al. (1982) designed,
constructed, and evaluated a greenhouse
line-source sprinkler system for use in examining
seedling response to a continuous water gradient.

The greenhouse installation is similar in
principle to the field line-source system except
that one spray nozzle moves along a fixed track
above a greenhouse ground bed.   The greenhouse
system provides a uniform gradient in water
application with high application rates directly
under the spray nozzle and low rates near the
outer edges of the ground bed.   Johnson et al.
(1982) reported that the automated greenhouse
line-source system was reliable and inexpensive,
could be used year-round, and was particularly
useful with seedlings.

Rumbaugh et al. (1983, 1984) used both the
greenhouse line-source system and the field
line-source system to evaluate the influence of a
water application gradient on seedling growth
responses.   The breeding implications of the study
by Rumbaugh et al. (1984) pertaining to cool-
season range grasses is summarized by Asay and
Johnson (this volume).   Basically, these studies
documented the usefulness of line-source sprinkler
systems in selecting forage breeding lines for
superior performance under drought.   The water
application gradient in both systems allows the
breeder to view the breeding lines' response to a
continuum of moisture levels, and offers
flexibility for picking a particular target
environment for selection.

Combination of Rainout Shelter and Line-Source
Sprinkler System

Another technique that is currently under
investigation by the USDA-ARS Forage and Range
Research Laboratory at Logan is the combined use
of a rainout shelter facility and a line-source
sprinkler system.   Rainout shelters cover and,
thus, exclude precipitation from field plots.
These shelters provide a field setting with strict
control over drought stress development.   Rainout
shelters are specifically built to minimize
disturbance to other environmental parameters such
as irradiation, temperature, and wind.   Typical
rainout shelters often cover a relatively small
area so that their application is limited to
small-plot studies.   However, large plot areas are
required in plant breeding and selection to
evaluate the large number of breeding lines.

The rainout shelter facility designed by Upchurch
et al. (1983) makes it possible to shelter a
relatively large plot area.   A similar facility
has been constructed at Logan.   This facility
covers approximately 0.08 ha and consists of two
moveable structures, each 21.7 m by 17.8 m.   These
two structures are located at opposite ends of a
plot and are moved automatically over the
plot area (43.4 m by 17.8 m) when precipitation is
detected.   The drive system for the facility is a
continuous cable that stretches from the far ends
of each shelter and which is wrapped over an
electric motor-driven steel drum in the center of
the plot area.   The direction of drum movement
determines whether the shelter opens or closes.
The two moveable shelters are mounted on steel
wheels that traverse three rails along the two
sides and center of the plot area.   This
dual-structure shelter was designed to operate

year-round and withstand the snow accumulation loads received at Logan. Such a design and year-round operation are critical in areas such as Logan where snowfall typically accounts for about 60% of yearly precipitation. The facility is currently being operated to exclude most of the rainfall and about 80% of the snowfall. Some snow is allowed to accumulate in the plots so the insulating influence of the snow and subsequent temperature relations of the plants and soil in the sheltered area are similar to those outside the shelter.

A line-source sprinkler system was developed for use in conjunction with the rainout shelter facility. The typical sprinkler head used in most line-source applications has a radial water distribution pattern of about 15 m, too great for the 8.9 m plot width under our rainout shelter. Consequently, sprinkler heads were systematically evaluated for use under our rainout shelter facility (Willardson et al. 1987), and those that produced suitable spray patterns and that fit within our desired plot width were installed.

One line-source sprinkler system was configured for each half of the rainout shelter facility. Each system is controlled separately so that each system can be used for different forages. The system and the rainout shelter provide an excellent facility for determining the influence of drought on the establishment, growth, and survival of range forage breeding lines. The rainout shelter excludes most precipitation from the plots, while the line-source sprinkler system adds known amounts of water back to the plots in such a way that a gradient of water is applied. The system imposes an entire gradient of drought levels and provides a more thorough analysis of plant response to drought than irrigated and nonirrigated plot comparisons. As a result, the particular level at which drought impacts the various breeding lines can be determined, and precise comparisons can be made among the breeding lines.

Stable Isotope Composition

Stable isotopes are nonradioactive forms of elements that occur naturally in the earth and its atmosphere. Because certain physical and biological processes show a distinct preference for or discrimination against different stable isotopes, stable isotopes can be used to evaluate physiological behavior in plants (Ehleringer et al. 1986). The stable isotopes of carbon hold particular promise for identifying plant genotypes capable of optimum production under water-limited conditions (Farquhar and Richards 1984).

There are two stable isotopes of carbon, ^{12}C and ^{13}C. Although about 99% of the carbon in the earth and its atmosphere is present as ^{12}C, the amount of ^{13}C in biological organisms varies due to discrimination by diffusional and enzymatic processes. Discrimination is particularly large in plants that fix carbon primarily by the C_3 pathway. Farquhar et al. (1982) proposed that this variation in ^{13}C discrimination in C_3 plants

depends on leaf intercellular carbon dioxide concentration (C_i). Data supporting this theoretical relationship now have been provided for a broad range of C_3 plants. C_i has been shown to be closely related to leaf stomatal conductance, which in turn is related to water use efficiency (amount of carbon gained compared to amount of water transpired). Even though the relationship between C_i, stomatal conductance, and water use efficiency has been known for some time, techniques have not been available to effectively and reliably evaluate these parameters over an extended period of time. Gas exchange procedures accurately measure these parameters, but generally only at one point in time. However, measurements of carbon discrimination can be used to estimate C_i and, therefore, stomatal conductance integrated over the development period of the plant. This integration capability may mean that measurements of carbon isotope discrimination will better separate physiological performance than most physiological assays.
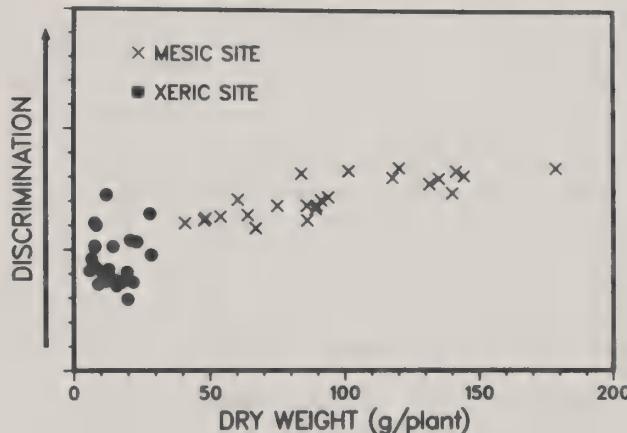
Figure 2. Relationship between carbon isotope discrimination and aboveground dry weight for eight species of range grasses grown at mesic and xeric sites with annual precipitation of 450 and 260 mm, respectively.

Studies with eight semiarid forage grass species and interspecific hybrids growing at a relatively mesic site (450 mm annual precipitation) and a xeric site (260 mm annual precipitation) in northern Utah indicate that the carbon isotope technique holds considerable promise for selection. The carbon isotope technique was used to analyze aboveground biomass. Analysis of these data indicated that significantly greater (P<0.05) discrimination against ^{13}C occurred on the mesic site than the xeric site. This discrimination was significantly (P<0.01) correlated with aboveground dry weight at the mesic site (r = 0.95), but not at the xeric site (r = -0.24) (fig. 2). Despite these differences in correlation, the relative differences in carbon discrimination among the forage grasses were similar at the two sites (r = 0.84). Thus, screening for carbon discrimination at one site may indicate performance at other sites. If this pattern is consistent also within

species, fewer sites will be required to assess the genetic variation in a breeding population. In addition, the coefficients of variation for the carbon discrimination measurements with three replications were 3.4% and 2.2% for the xeric and mesic sites, respectively. Such precision suggests that relatively small genetic differences can be detected. The precision of the carbon discrimination measurement and the apparent consistency between sites suggests that the carbon isotope technique may increase the effectiveness and reduce the time required to screen large populations for response to water-limited environments.

FUTURE OUTLOOK

The future development of techniques to screen range forage breeding lines for improved seedling establishment will involve identifying procedures that more closely simulate field conditions or techniques that allow for greater control in the field. The closer the screening procedures simulate field establishment conditions, the more likely these procedures will identify breeding lines with better seedling establishment in the field. However, these procedures must be able to reduce climatic variations so that performance of the breeding lines can be compared from one year to the next. Techniques that consistently reproduce the test environment are required to achieve optimum selection progress.

LITERATURE CITED

Asay, K. H., D. R. Dewey, F. B. Gomm, D. A. Johnson, and J. R. Carlson. 1985a. Registration of 'Bozoisky-Select' Russian wildrye. Crop Sci. 25:575-576.

Asay, K. H., D. R. Dewey, F. B. Gomm, D. A. Johnson, and J. R. Carlson. 1985b. Registration of 'Hycrest' crested wheatgrass. Crop Sci. 25:368-369.

Asay, K. H. and D. A. Johnson. 1980. Screening for improved stand establishment in Russian wild ryegrass. Can. J. Plant Sci. 60:1171-1177.

Asay, K. H. and D. A. Johnson. 1983. Genetic variability for characters affecting stand establishment in crested wheatgrass. J. Range Manage. 36:703-706.

Ashton, T. 1948. Techniques of Breeding for Drought Resistance in Crops. Commonwealth Bur. Plant Breed. Genet., Tech. Commun. No. 14. Aberystwyth.

Ehleringer, J. R., P. W. Rundel, and K. A. Nagy. 1986. Stable isotopes in physiological ecology and food web research. Tree 1:42-45.

Farquhar, G. D., M. H. O'Leary, and J. A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9:121-137.

Farquhar, G. D. and R. A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust. J. Plant Physiol. 11:539-552.

Hanks, R. J., J. Keller, V. P. Rasmussen, and G. D. Wilson. 1976. Line source sprinkler for continuous variable irrigation-crop production studies. Soil Sci. Soc. Am. J. 40:426-429.

Johnson, D. A. 1980. Improvement of perennial herbaceous plants for drought-stressed western rangelands. p. 419-433. In: Turner, N. C. and P. J. Kramer (eds.). Adaptation of Plants to Water and High Temperature Stress. Wiley-Interscience, New York.

Johnson, D. A. 1986a. Improved rangeland species: a physiological perspective. p. 444-446. In: Joss, P. J., P. W. Lynch, and O. B. Williams (ed.). Rangelands: A Resource Under Siege. Australian Academy of Science, Canberra.

Johnson, D. A. 1986b. Seed and seedling relations of crested wheatgrass: a review. p. 65-90. In: Johnson, K. L. (ed.) Crested Wheatgrass: Its Values, Problems and Myths; Symposium Proceedings. Utah State Univ., Logan.

Johnson, D. A. and K. H. Asay. 1978. A technique for assessing seedling emergence under drought stress. Crop Sci. 18:520-522.

Johnson, D. A., M. D. Rumbaugh, and K. H. Asay. 1981. Plant improvement for semi-arid rangelands: possibilities for drought resistance and nitrogen fixation. Plant and Soil 58:279-303.

Johnson, D. A., M. D. Rumbaugh, L. S. Willardson, K. H. Asay, D. N. Rinehart, and M. R. Aurasteh. 1982. A greenhouse line-source sprinkler system for evaluating plant response to a water application gradient. Crop Sci. 22:441-444.

Levitt, J. 1972. Response of Plants to Environmental Stress. Academic Press, New York. 697 pp.

Rumbaugh, M. D., K. H. Asay, and D. A. Johnson. 1984. Influence of drought stress on genetic variances of alfalfa and wheatgrass seedlings. Crop Sci. 24:297-303.

Rumbaugh, M. D., D. A. Johnson, and D. N. Rinehart. 1983. Stand density, shoot weight, and acetylene reduction activity of alfalfa populations subjected to field and greenhouse moisture gradients. Crop Sci. 23:784-789.

Stoddart, L. A., A. D. Smith, and T. W. Box. 1975. Range Management. McGraw-Hill, New York.

Upchurch, D. R., J. T. Ritchie, and M. A. Foale.
1983. Design and use of a dual-structure
rainout shelter. Agron. J. 75:845-848.

Willardson, L. S., D. M. Oosterhuis, and
D. A. Johnson. 1987. Sprinkler selection for
line-source irrigation systems. Irrig. Sci.
(In Press).

Wright, L. N. 1964. Drought tolerance - program-
controlled environmental evaluation among range
grass genera and species. Crop Sci. 4:472-474.

Wright, L. N. 1971. Drought influence on
germination and seedling emergence. p. 19-44.
In: Larson, K. L. and J. D. Eastin (eds.).
Drought Injury and Resistance in Crops. Crop
Sci. Soc. Amer. Spec. Publ. No. 2. Madison,
Wisconsin.

COMPETITION AND PLANT ESTABLISHMENT

M. J. Samuel[1] and E. J. DePuit[2]

ABSTRACT

Inter- and intraspecific competition is a synecological interaction that strongly influences plant establishment following range seeding. Plant density, innate competitive ability (influenced by physiology or morphology), and resource abundance are factors which affect competition. Some of these factors can and should be manipulated in range reseeding efforts to enhance plant establishment.

INTRODUCTION

Competition between organisms has been of interest to scientists at least since the writings of Darwin (1872). Competition was recently defined as "the induction of strain in one organism as a result of the use, defense or sequestering of resource items by another organism" (Welden and Slauson 1986). Competition influences not only interactions among established plants but also plant establishment.

Competition is dependent upon the proximity of organisms. Theoretical or experimental models of species growth in isolation, therefore, will not predict the outcome of a struggle for existence between species (Harper 1977). Successful plant establishment requires consideration of synecological as well as autecological attributes of plants. Competition is one of the more important synecological interactions.

This paper will briefly review principles of competition between plants and the factors that control this interaction. Selected research on the influence of specific factors on competition and plant establishment will be discussed in greater detail.

BACKGROUND

Competition and its effects on plant establishment are governed both endogenously and exogenously (i.e., by both plant-related and external factors). It is the interaction of these factors that should be considered in any given situation. The following paragraphs briefly describe the influence of selected factors on competition. More comprehensive reviews are available elsewhere (e.g. Harper 1977, Risser 1969).

---

[1] Botanist, USDA-ARS, High Plains Grasslands Research Station, 8408 Hildreth Rd., Cheyenne, Wyoming 82009.
[2] Associate Professor, Range Management Department, University of Wyoming, P.O. Box 3354, University Station, Laramie, Wyoming 82071.

Endogenous Factors Affecting Competition

Seed and Seedling Morphology

Differences in seed morphology may be a factor affecting competitive relationships when planting mixtures of species. Larger seeded species may have more seed capital (embryonic weight plus some fraction of the endospermic reserves) with a potential of competitive advantage over smaller-seeded species (Harper 1977). Seed anatomy and presence of attached structures may influence germination requirements and rates (Copeland 1976). This may indirectly affect competition among species through differential timing of initial seedling growth.

Above- and below-ground seedling size can strongly influence their ability to compete for resources. The seedling with the highest canopy or the most extensive root system may have the advantage. A plant may have the highest canopy because of morphological traits such as the longest hypocotyl, the longest petioles, or the longest internodes (Harper 1964).

Rooting pattern is determined by the genetic attributes of the species. Nevertheless, there is no evidence to support the premise that roots of one plant can interfere with or exclude roots of another plant from a soil zone (Harper 1977). Litav and Harper (1967) grew paired plants of oats (Avena) or one oat and one pea (Pisum). Vertical distribution of roots was random between plants of similar and different species. Ellern et al. (1970) grew two species of oats in pure stand or in mixture. Each species had a pattern of depth stratification which was not changed by growth with the other species.

Seed and Seedling Physiology

Grubb (1977) listed physiological controls of the timing of seed germination: temperature responses, hard seed coat breakdown, inhibitor leaching, hydration differences necessary for germination, and changes which occur during after-ripening or from burial. These requirements may be quite different among species in mixtures and may influence the ultimate outcome of competition. Temporal advantages may be afforded to the first species which germinates, making it more competitive if adequate conditions for growth occur following germination.

Although species with differing photosynthetic pathways are able to coexist in the same habitat (Kemp and Williams 1980), varying temperature requirements for germination and seedling growth may leave one species at a disadvantage during certain portions of the growing season. This should be expected between C_3 and C_4 species, but it cannot always be predicted from the pathway. Optimum temperature ranges can sometimes overlap across pathways (Sabo et al. 1979, Young and Evans 1982).

Photosynthetic pathways can be important determinants of inherent rates and patterns of plant growth. C_3 plants have more efficient

photosynthesis at low temperatures and high water availability. C_4 plants are more efficient in photosynthesis and water use when temperatures are high and water availability is limiting (Edwards and Walker 1983). A faster growth rate can give one species a competitive advantage of increased size (Harper 1977). Despite these differences, seasonal temperature gradients may induce offsetting patterns of resource utilization and therefore decrease interspecific competition between C_3 and C_4 species (Monson et al. 1983).

Density

Density of established plants in nature follows a logistic curve. Density initially increases rapidly and linearly, but the rate of increase eventually declines. Ultimately, density becomes constant at the the point where recruitment and mortality rates become equal. Density has a direct effect on the resource availability of a plant. As density increases, the area in which the plant can obtain resources decreases. Under ideal germination conditions or if a timely increase in resource availability occurs, a high density may result. This may be detrimental and cause high plant mortality (Harper 1977) because of increased intensity of competition from the close proximity of plants competing for resources.

Exogenous Factors Affecting Competition

Competition and its effects on plant establishment may be modified by external factors. Most exogenous influences on competition can be directly or indirectly related to the abundance of resources for which plants compete.

Competition by definition relates to the interaction among plants to obtain needed resources. It follows that the availability of resources must at least partially govern the intensity and effects of competition. Risser (1969) listed water, nutrients, light, oxygen, carbon dioxide, and agents of pollination and propagule dispersal as resources for which plants may compete in grassland ecosystems. Considerable debate has raged over the relationship of resource abundance to competition (Welden and Slauson 1986). Certain ecologists, both early (Darwin 1872) and recent (Wiens 1977), support the postulate that competition is intensified by resource scarcity. Conversely, others (Huston 1979, Grime 1979, Wilson and Keddy 1986) have argued that as resources become more abundant, differences in competitive ability among plants become more manifest and, consequently, more strongly influence plant community composition and function. Welden and Slauson (1986) felt that much of this controversy was due to lack of distinction, by ecologists, between the intensity and the importance (i.e., results) of competition.

Recent revegetation research lends credence to the concept that at least the results of competition, if not necessarily its intensity, are accentuated under conditions of increased resource availability. Biondini and Redente (1986) noted

reductions in plant community diversity concomitant with improved plant growth conditions (i.e., with fertilization and improved soil quality) and attributed this to effects of greater interspecific competition under reduced resource stress. DePuit et al. (1982) noted a similar relationship with respect to water availability, in which the apparent competitive inhibition of certain species was greater under irrigated than under nonirrigated conditions. These results suggest that species with high competitive ability are best able to exploit a resource, to the detriment of their less competitive neighbors, under conditions of increased resource availability. Under lower resource availability, other plant attributes, such as stress tolerance and/or avoidance, may become more important to plant survival than competitive ability (Grime, 1979).

"Disturbance" may be defined as any discrete event that disrupts biological structure in ecosystems and changes resource availability or physical environment (White and Pickett, 1985). Disturbances may include such disparate phenomena as grazing, fire, pathogens or disease, short-term drought, and other catastrophic events. If disturbances occur immediately before or soon after seed germination, they can influence plant establishment by altering competitive interactions among plants. Denslow (1985) felt that disturbances can alter competition in at least two ways. First, disturbances may directly impact plants themselves, thereby affecting their innate competitive ability. Second, and more relevant to our present discussion, disturbances may indirectly or directly alter resource abundance, thus influencing competition in ways described previously.

In cases where the number of plants is reduced by a disturbance but resources are not adversely impacted, the disturbance may in effect increase resource availability to the remaining plants. An example of this would be tillage. Other types of disturbance (e.g., rangeland fertilization) may directly increase resource abundance. Whenever disturbances increase resource abundance, the net effect may be to increase competition and/or expression of the results of competition on plant establishment.

Other types of disturbance, such as accelerated erosion or catastrophic events, may be of a sufficient magnitude to reduce resources as well as plants. In such cases, competition may not be as biologically important in influencing plant establishment as other factors (e.g., stress tolerance or avoidance attributes of plants).

SELECTED RESEARCH

Endogenously-Modified Competition and Establishment

Example 1: Density

A mined land revegetation study in Montana (DePuit

et al. 1980)[3] demonstrated the effects of plant density on competition and plant establishment. Part of this study involved broadcasting a mixture of 13 native perennial grasses at three total mixture seeding rates (650, 975, and 1300 PLS m^{-2}). Seeding rates were identical for each species in each mixture-rate treatment (50, 75 and 100 PLS m^{-2} species^{-1}). Initial plant establishment was considered complete at the end of the second growing season.

Plant density progressively increased with increasing seeding rate (fig. 1b), but total grass biomass remained statistically similar across seeding rates (fig. 1a). Total biomass did not increase because of a significant decline in individual plant biomass at the highest seeding rate (fig. 1c). It is also noteworthy that percent establishment of perennial grasses (density/seeding rate) consistently declined with increasing seeding rate (fig. 1b).
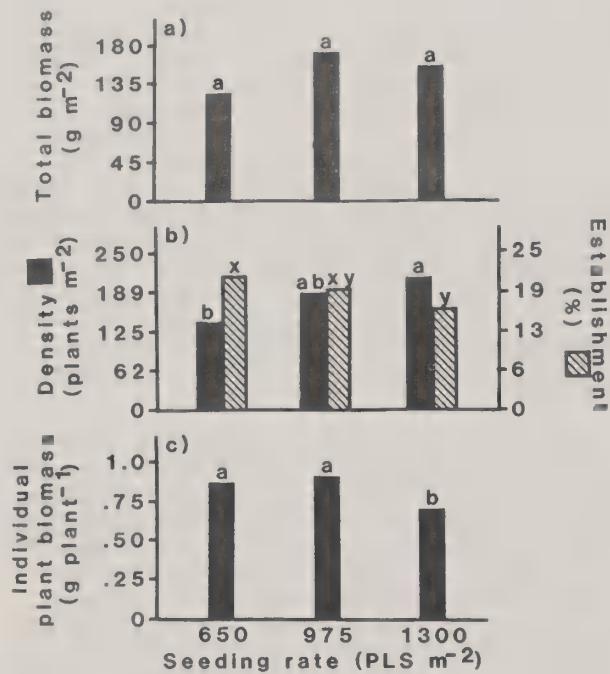
Figure 1. Effect of varied seeding rates (650, 975, and 1300 PLS meter^{-2}) on second-year: a) total biomass, b) total density and percent establishment (density/seeding rate x 100), and c) individual plant biomass (total biomass /density) for seeded species. Bars for a given attribute with the same letter are not significantly different (P≤0.05).

Figure 2a portrays individual species canopy cover responses to seeding rate during the second

growing season. Cover of thickspike wheatgrass (Agropyron dasystachyum [Hook.] Scribn.) progressively increased with seeding rate. Cover of western wheatgrass (A. smithii Rydb.) and slender wheatgrass (A. trachycaulum [Link.] Malte) remained statistically similar across seeding rates. Green needlegrass (Stipa viridula Trin.) cover declined significantly at the heaviest seeding rate. Combined cover of 9 subdominant perennial grasses declined with the first increase in seeding rate. Perennial grass diversity (Shannon-Wiener Index, Shannon and Weaver 1973, fig. 2b) also declined with increasing seeding rates, particularly at the highest seeding rate.
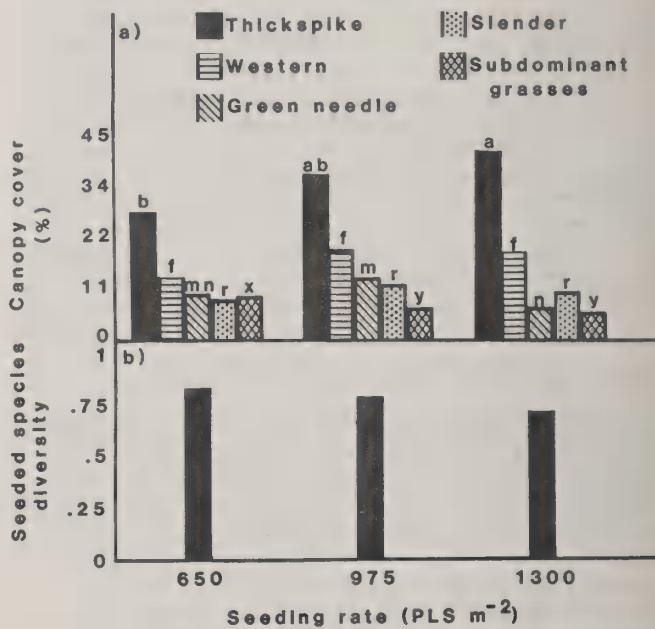
Figure 2. Effects of varied seeding rates (650, 975, and 1300 PLS m^{-2}) on second-year: a) canopy cover of seeded perennial grass species, and b) seeded species diversity (Shannon-Wiener Index), Colstrip, MT, 1978. For canopy cover, bars within species or species group with the same letter are not significantly different (P≤0.05).

Example 2: Innate competitive ability

Results of two similarly designed but geographically separate studies provide insight on the influence of innate competitive ability. In a mined land revegetation study at Colstrip in southeastern Montana[4], 12 perennial grass species were similarly broadcast in monoculture (600 PLS m^{-2} species^{-1}) and all possible two-species combinations (300 PLS m^{-2} species^{-1}). Data from thickspike wheatgrass, intermediate wheatgrass [A. intermedium (Host) Beauv.], and western wheatgrass

---

[3] also DePuit unpublished.

[4] DePuit unpublished

were analyzed to reflect differences in inherent vigor. These 3 species have similar rhizomatous morphology and cool-season physiology. In a competition study near Cheyenne in southeastern Wyoming[5], these same three wheatgrasses were drill seeded in monoculture and in all possible two-species combinations. Seeding rates for pure stands were 200, 250, and 260 PLS for intermediate, western, and thickspike wheatgrasses, respectively. Each species was planted at half

a) Intermediate wheatgrass

b) Thickspike wheatgrass

c) Western wheatgrass

Individual plant biomass (g plant^{-1})

Competing species

Figure 3. Effect of competing species on second year individual plant biomass of intermediate wheatgrass (Agin), thickspike wheatgrass (Agda) and western wheatgrass (Agsm) grown in monoculture and two-species combinations: Colstrip, MT (solid bars) and Cheyenne, WY (hatched bars). Bars within a species with the same letter are not significantly different ($P \leq 0.05$ for Colstrip, $P \leq 0.10$ for Cheyenne).

5 Samuel unpublished

that rate in combination plots. Both studies were conducted on sandy-loam soils in areas receiving approximately 35 cm precipitation per year.

Figure 3 presents second-season individual plant biomass (total biomass/density), for the Colstrip and Cheyenne studies for each species growing alone and in combination with each of the other two species. Intermediate wheatgrass was more competitive than western wheatgrass at both sites. Intermediate wheatgrass had higher individual plant biomass when grown with western wheatgrass (fig. 3a). At Cheyenne, thickspike wheatgrass had higher individual plant biomass when grown with either intermediate or western wheatgrasses than when grown alone; intraspecific competition was very intense (fig. 3b). At Colstrip, thickspike wheatgrass was generally between western and intermediate wheatgrasses in competitive ability (fig. 3a, b, c). At Colstrip, western wheatgrass plants had lower individual plant biomass when grown with intermediate wheatgrass than when in pure stand (fig. 3c).

Blue grama (Bouteloua gracilis [H.B.K.] Griffiths), a warm-season grass, was also sown alone and in combination with other species at Cheyenne. Blue grama establishment was not good and was less than half of that of the wheatgrasses. Nevertheless, important relationships are apparent in the data. Blue grama had the highest production in monoculture. When grown with concurrently seeded cool-season wheatgrasses, blue grama production was reduced (fig. 4).

Blue grama

Total biomass (kg ha^{-1})

Competing species

Figure 4. Effects of competing species on second-year biomass of blue grama sown in monoculture and in two-species combinations with thickspike wheatgrass (Agda), intermediate wheatgrass (Agin), and western wheatgrass (Agsm), Cheyenne, WY. Bars with the same letter are not significantly different ($P \leq 0.05$).

Data were taken at Cheyenne on nonseeded species which volunteered within the seeded plots. Maximum production of nonseeded species occurred in monoculture plots of blue grama. Conversely,

TABLE 1.   Biomass of nonseeded species in plots seeded to monocultures or various two-species
          combinations, Cheyenne, WY.

Seeded species:	Growing in combination with seeded species:			
	Thickspike wheatgrass	Intermediate wheatgrass	Western wheatgrass	Blue grama
	--------------Non-seeded species (kg ha^{-1})-----------			
Thickspike wheatgrass	399 abc[1]	149 a	249 ab	463 abc
Intermediate wheatgrass	----	331 abc	195 a	319 ab
Western wheatgrass	----	----	476 abc	1278 bcd
Blue grama	----	----	----	1852 d

[1] Values with the same letter are not significantly different (P≤0.05).

nonseeded species production was lowest in plots
where thickspike and intermediate wheatgrasses
were planted with the blue grama, with each other,
or with western wheatgrass (Table 1).

Exogenous Influences on Competition and
    Establishment

Competition is always modified by variations in
endogenous factors. Exogenous factors may also
indirectly modify competition through their
influence on endogenous factors. For example, a
change in resource abundance may change the effect
of endogenous factors (e.g., density, relative
competitive ability among species, etc.) and
thereby alter competitive relationships during the
establishment phase. Three research-derived
examples will illustrate the influence that
variation in exogenous factors can have.

    Example 3: Water availability and seeding date

Results of a mined land irrigation, seeding date
study in Montana (DePuit 1980, Young and Rennick
1982) indicate how variation in water availability
and timing of seeding can influence competitive
ability and establishment of cool- and warm-season
species.

This study, in brief, investigated effects of
varied seeding dates and supplemental irrigation
regimes on establishment of a given mixture of
cool- and warm-season perennial grasses. Seed was
planted in the early spring or the early summer.
Additional water was applied by sprinkler at
approximately 15 cm month^{-1} for 0, 1 or 2 summer
months. Data were collected after the first
growing season. Without supplemental summer
irrigation, spring seeded cool-season grasses had
more canopy cover than spring seeded warm-season
grasses (fig. 5a). Cover of both cool- and
warm-season grasses was negligible under summer
seeding with no irrigation (fig 5b).

Although summer irrigation was intentionally
applied to promote growth of the spring-seeded
warm-season grasses, additional water increased

the cover only of the cool-season grasses. Summer
seeding with irrigation to overcome seasonal
drought favored warm-season grasses, although
overall vegetation establishment still did not
equal that under spring seeding.
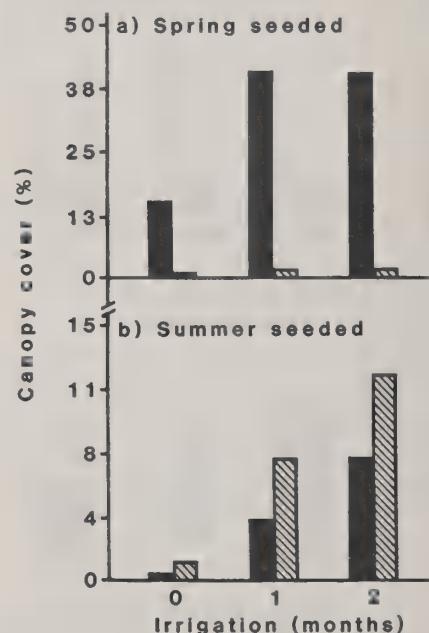

Figure 5.   Effects of irrigation for 0, 1, or 2
           months on percent canopy cover of cool-
           season grasses (solid bars) and
           warm-season grasses (hatched bars) with
           a) spring seeding and b) summer
           seeding, Colstrip, MT.

    Example 4: Opening size

A field study[6] was initiated to investigate the

---

[6] Samuel unpublished

effect of opening size (i.e., spatial resource abundance) within a western wheatgrass sod on the establishment of 'Hachita' blue grama seedlings. In the spring, one month old blue grama seedlings were transplanted into circular openings of 0, 4, 8, or 16 cm diameter. For the 0 cm opening, no root material was removed and a rod was pushed into the soil far enough to make a slit large enough for the blue grama seedling plug. For all other opening sizes, soil-root cores of the corresponding diameter were removed to a depth of approximately 30 cm. Holes were refilled with soil as the seedling plugs were planted. This procedure was repeated on fallow ground to insure that differences were from competition and not the result of changes in soil physical characteristics.

By the end of the first growing season, significantly fewer plants had survived in the smallest opening than in all the larger openings in the sod and all openings in the fallow planting (fig. 6). There was no significant loss of plants after the second growing season in the western wheatgrass sod. An open, warmer-than-normal winter apparently allowed drying of the fallow soil where 85% of the plants died across all opening sizes.
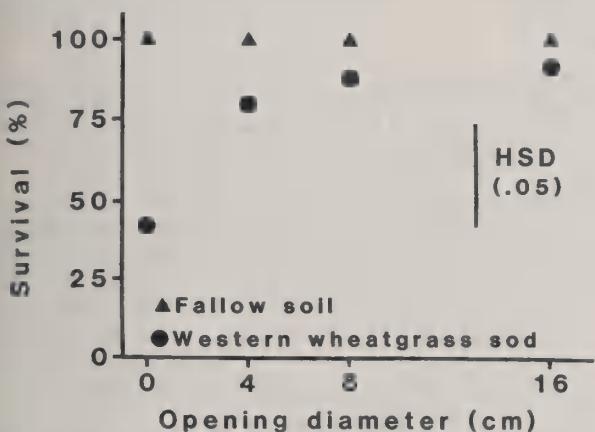

Figure 6. First growing season survival of blue grama seedlings in openings (0, 4, 8, and 16 cm diameter) in fallow soil and western wheatgrass sod, Cheyenne, WY.

Example 5: Fertilization

Selected results of a fertilization study on southeastern Montana mined land (DePuit and Coenenberg 1979) illustrate effects of nutrient-resource abundance on competition and plant establishment. A level site covered with 10 cm of sandy loam, nitrogen (N) deficient (2.2 ppm NO_3-N) topsoil was uniformly seeded to a mixture of 9 perennial grasses, 4 legumes and 3 shrubs. Nitrogen fertilization rates of 0, 37, 74, and 121 kg N ha^{-1} year^{-1} were applied. These four treatments represent progressively increasing levels of nutrient resource abundance. Second growing season vegetation data reflected plant establishment in response to treatments.

Figure 7a indicates that total aboveground biomass

significantly increased from 0 to 37 kg N ha^{-1}, but remained constant at 37, 74 and 121 kg N ha^{-1}. Response patterns for classes of vegetation (seeded perennial grasses, legumes, and nonseeded annual forbs) differed. Total perennial grass and annual forb biomass progressively increased from 0 to 121 kg N ha^{-1}, and many of these increases were significant. In contrast, total legume biomass was constant at 0 and 37 kg N ha^{-1}, and subsequently declined at 74 and 121 kg N ha^{-1}.

Analysis of plant density and individual plant biomass data may help to explain variations in competition among treatments. Perennial grass density (fig. 7b) consistently increased with fertilization rate, while individual plant biomass only increased from 0 to 37 kg N ha^{-1}. Annual forb density was lowest at 0 and 37 kg N ha^{-1} and significantly increased to maximal levels at the two highest fertilization rates. Individual plant biomass data for annual forbs followed exactly the opposite pattern.

Legume density was statistically similar at 0 and 37 kg N ha^{-1} and was significantly reduced at the two highest N fertilization rates (fig. 7b). Individual plant biomass of legumes increased from 0 to 74 kg N ha^{-1} before declining at 121 kg N ha^{-1} (fig. 7c).

An analysis of canopy cover data of the major seeded perennial grass and legume species provides insight on which individual plant species accounted for the plant-class responses. Among grasses (fig. 8a), crested wheatgrass (Agropyron cristatum [L.] Gaertn.) changed most markedly. Canopy cover of crested wheatgrass increased with increasing fertilization. Green needlegrass cover progressively increased with fertilization to a point (74 kg N ha^{-1}) and then leveled off at 121 kg N ha^{-1}. Smooth brome (Bromus inermis Leyss.) cover did not significantly increase until fertilized at 121 kg N ha^{-1}. Combined cover of other, subdominant grasses progressively increased up to 74 kg N ha^{-1}, but significantly declined at 121 kg N ha^{-1}. Among legumes (fig. 8b), cover of both cicer milkvetch (Astragalus cicer L.) and yellow sweetclover (Melilotus officinalis [L.] Lam.) was reduced by fertilization, but cicer milkvetch declined both sooner and more markedly than did yellow sweetclover. Cover of alfalfa (Medicago sativa L.), although lower than that of the other two legumes, was unaffected by fertilization.

DISCUSSION

The research reviewed indicates that competition during the seedling stage can strongly influence plant establishment, and that the nature of this influence is governed by an interacting array of endogenous and exogenous factors. Success in range seeding, therefore, depends in part upon proper understanding of the effects of competition during the establishment phase and the factors that modify this phenomenon. Competition and its influence can be manipulated by appropriate modification of endogenous and exogenous factors.
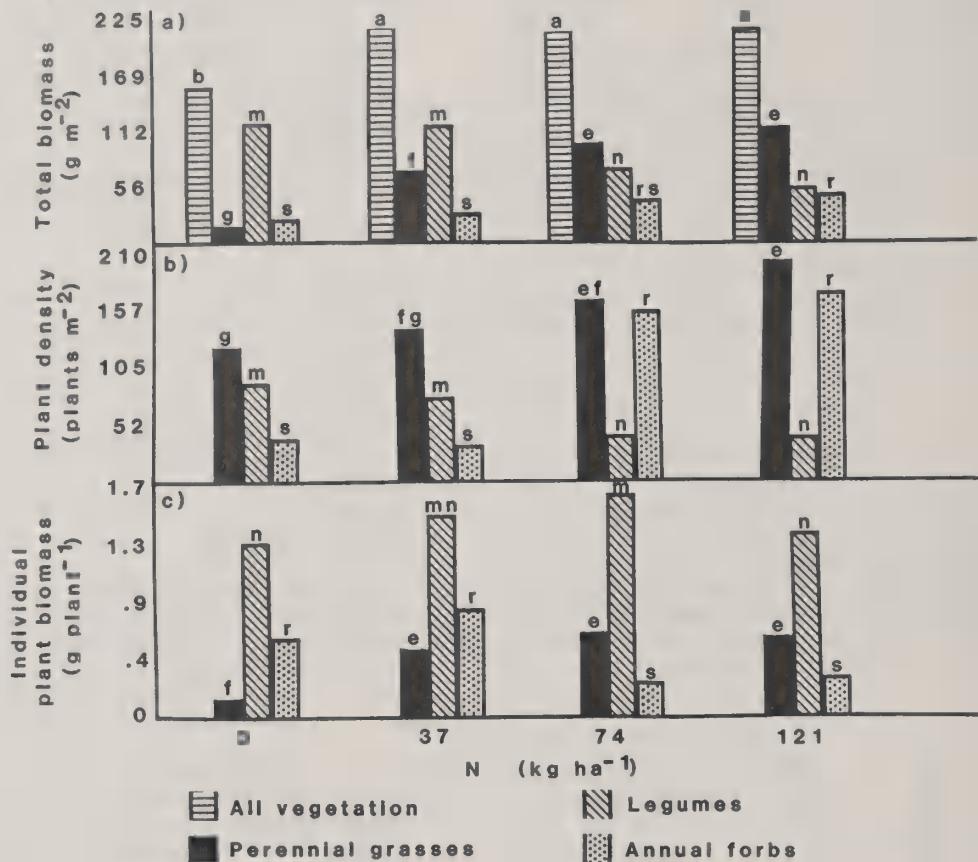
Figure 7. Effects of N fertilization rate (0, 37, 74, and 121 kg N ha^{-1}) on a) total biomass, b) plant density, and c) individual plant biomass (total biomass/density) of seeded species, Colstrip, MT. Bars within each species group with the same letter are not significantly different (P$\leq$0.05).
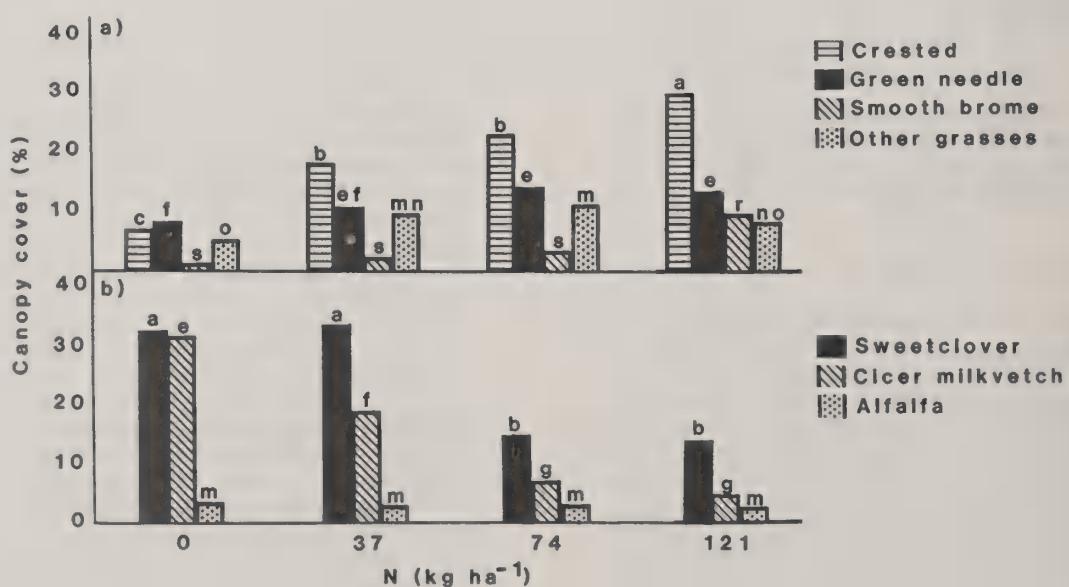
Figure 8. Canopy cover under differential N fertilization (0, 37,74, and 121 kg N ha^{-1}) for a) perennial grasses, and b) legumes, Colstrip, MT. Bars within each species with the same letter are not significantly different (P$\leq$0.05).

Intensity and effects of competition are accentuated at higher plant densities. The endogenous factor of density many be manipulated in a number of ways. Density may be directly influenced by seeding rate (fig. 1). Excessive seeding rates may have no significant benefit on total stand productivity, but may produce a density-induced reduction in individual plant biomass. Higher plant density also decreased percent plant establishment in probable response to increased competition stress between plants (fig. 1).

The results of the density study also indicate that innate competitive ability was influenced by density effects. Not all perennial grasses responded similarly to seeding rate/density-induced differences in competition (fig. 2a). Species with higher innate competitive ability increased in abundance in response to seeding rate. Species with lower inherent competitive ability were eventually retarded by more responsive species as seeding rates and hence plant densities increased. This density-dependent increase in competitive exclusion was reflected in the decline of seeded grass diversity as seeding rates increased (fig. 2b). Overly heavy seeding rates should be avoided in situations were mixed stands are desired, since at resultant high densities species with lower competitive ability may be retarded (fig. 2).

Another approach to reducing negative effects of high density on establishment involves increasing the distance between a plant and its nearest competitor, as results of the blue grama sod transplant study indicate (fig. 6). In addition to removing competing vegetation (with mechanical means, herbicides, prescribed burning, etc.) prior to seeding, the proximity of competing species may be reduced by planting seeds of different species into different microsites. Various techniques may accomplish this, such as separately planting different species in different furrows with a drill seeder, planting alternating drill strips with monocultures of different species, or perpendicular cross-drilling of different species. While these approaches will certainly reduce interspecific competition, density-dependent intraspecific competition will nonetheless be a concern. Therefore, care must still be taken not to seed at overly high rates.

Research reviewed (examples 1, 2, and 5) also demonstrated that innate differences in competitive ability among species may strongly influence competitive interactions and, therefore, establishment among species in mixtures. A brief review of characteristics (Wasser 1982, Brown and Wiesner 1984) of species used in our examples yields clues on why their seedling competitive ability varied. Intermediate, thickspike and western wheatgrasses are all C_3 species with similar gross morphology and phenology. The relatively high competitive abilities of intermediate and thickspike wheatgrasses may be related to large seed size, relative ease and rapidity of germination, good seedling vigor, high production potential, and/or environmental adaptation. Conversely, the relatively poor

competitive ability of western wheatgrass (in the seedling stage) may be due to its moderate germinative ability, seedling vigor and production potential, and/or lower adaptation to sandy soils. Blue grama has very poor seedling competitive ability. This could be related to small seed size, poor seedling establishment because of unique seedling morphology (Hyder et al. 1971), and moderate to low production potential. Blue grama also differed from the other three species morphologically and physiologically, because it is a sod-forming bunchgrass with C_4 photosynthesis.

For the above reasons and due to a spring seeding date at Cheyenne (example 2), blue grama establishment was poor in comparison to that of cool-season grasses. Nevertheless, blue grama had the highest production in monoculture (fig. 4) and, therefore, is a good intraspecific competitor. As indicated by its reduced productivity in combination with most cool-season grasses, however, it is a poor interspecific competitor.

If possible, differences in competitive ability among species should be considered when mixtures of seeded species are composed. Consideration also should be given to nonseeded species which may potentially be important competitors (Table 1). Ideally, all species in a given seeded mixture should be "compatible". They should have the same seedling competitive ability. In reality, this ideal will rarely, if ever, be achievable. Species in mixtures will usually differ in competitive ability, and less competitive species may be reduced by concurrently establishing species with higher competitive ability (figs. 3 and 4, Table 1). If it proves necessary to establish species with differing competitive and/or germination attributes, properly applied seeding methods and other cultural practices may sometimes compensate for such interspecific differences. For example, data of figure 5 demonstrated that both warm and cool season grasses could be established concurrently by employing a later seeding date if summer water availability was adequate. Another and perhaps more feasible approach involves temporally staggered seeding dates for different species in a mixture. Autecologically disparate species may be sown separately during their respective "optimum" periods in the growing season. A variant of this approach involves sowing less competitive species first, allowing sufficient time for establishment, and later interseeding more competitive species (Coenenberg 1982). A final practice involves sowing highly competitive species in a mixture at lower rates than their less competitive counterparts, thereby reducing their competitive impact through lower seedling density (DePuit 1982). This approach, however, has not always proved effective (Doerr et al. 1983).

Results of the N fertilization study (figs. 7 and 8) indicated that exogenous factors such as N abundance can markedly influence competition and plant establishment. During the plant establishment phase, variations in N fertilization may alter both individual plant size and the density or production of the stand as a whole.

Individual plant biomass was reduced under lowest N fertilization (fig. 7c). This may have been due to direct stress on plants caused by reduced N availability or water-use efficiency, or due to increased competition stress. The former explanation is more plausible because density of most plants was also reduced under lowest resource abundance. The only exception to this was legume density which was highest under nonfertilization and low N (fig. 7b). This could be interpreted that legumes have greater competitive ability relative to other species. This is probably not true because individual plant biomass of legumes was reduced under lowest N abundance (fig. 7a). If individual plant biomass is indeed an indicator of competitive ability, perhaps legumes simply were more tolerant rather than more competitive under N-limiting conditions. Legumes may have greater tolerance of low soil N because of N-fixing ability.

Perennial grass density (fig. 7b) progressively increased with fertilization rate, while individual plant biomass only increased with 0 to 37 kg N ha^{-1}. The competitive advantage conferred to grasses by increasing N fertilization was therefore primarily due to increased plant density. Annual forb density was lowest at 0 and 37 kg N ha-1 and significantly increased to maximal levels at the two highest fertilization rates. Individual plant biomass for annual forbs followed exactly the opposite pattern. Thus, the competitive advantage of annual forbs at higher N fertilization was entirely related to higher density. The decline in individual plant biomass of annual forbs at higher fertilization was presumably due to increases in intra- and inter-plant class competition induced by higher plant density.

In the fertilization study, density, individual plant productivity and cover (fig. 8b) of less N-responsive legumes were all lowest under highest N fertilization, as was cover of subdominant perennial grasses (fig. 8a). This indicates that competitive retardation or exclusion of less responsive by more responsive species may be greatest under conditions of high resource abundance. This relationship is supported by the eventual (4th growing season) reduction of vegetation diversity under highest N rates (DePuit and Coenenberg 1979).

Resource abundance relationships have important implications for range seeding. It is sometimes necessary to apply cultural practices that increase resource availability (e.g., range fertilization) to promote plant establishment. Our results suggest that N should be applied only at levels sufficient to promote plant establishment but not so high as to significantly increase plant competition. This principle is especially pertinent in situations where maximum uniformity among seeded species is desired. It may also apply to monoculture plantings, since increased resource availability may also increase competition pressure from nonplanted, indigenous or invading species (such as annual weeds, fig. 7).

We have intentionally limited our discussion to the role of competition during the plant establishment phase. It must be at least recognized, however, that the ultimate success of range seeding will also depend upon synecological relationships and changes expressed over longer periods of time (i.e., succession). DePuit and Redente (1986) noted that reseeded sites are usually dynamic rather than static in years following initial establishment. This dynamism depends not only upon the nature of initial revegetation practices and plant establishment, but also upon subsequent site management. Thus, longer term synecological relationships (including the influence of competition) need to be considered in concert with those related to the establishment phase.

CONCLUSIONS

Plant establishment is governed not only by seed and seedling autecology, but by synecological interactions among plants during the establishment phase. As indicated by research reviewed in this paper, competition is an especially important type of synecological interaction that can influence plant establishment. Competition and its effects on establishment are influenced by a complex, interacting array of endogenous and exogenous factors. Research results have shown that endogenous factors such as plant density and innate competitive ability of species (as governed by autecological attributes) will influence establishment. Furthermore, endogenous influences on competition and establishment can be modified by exogenous variables such as resource abundance. These factors can be manipulated by varying the species, seeding methods and cultural practices employed in range seeding, thereby affording an opportunity to modifying competition. As a consequence, plant establishment can be enhanced.

There is a tendency in plant establishment research and application to emphasize only autecological characteristics and requirements of species to be planted. While seed/seedling autecology is certainly important and must be properly addressed, we feel synecological propriety in range seeding methods is at least equally essential to promote success. Ignorance of plant interactions, such as competition, may often lead to partial or complete failure of reseeding efforts -- even if all autecological requisites for establishment among seeded species have been met.

LITERATURE CITED

Biondini, M. E. and E. F. Redente. 1986. Interactive effect of stimulus and stress on plant community diversity in reclaimed lands. Reclam. Reveg. Res. 4:211-222.

Brown, G. A. and L. E. Wiesner. 1984. Selecting species for revegetation: a guide for disturbed lands in the western coal region. MT Agric. Exp. Sta. Special Rep. 3, Bozeman.

Coenenberg, J. G. 1982. Methods for establishment of diverse native plant communities at the Rosebud Mine. pp. B6(1)-B6(20). In: F. F. Munshower and S. E. Fisher (eds.). Proceedings: Symposium on surface coal mining and reclamation in the Northern Great Plains. MT Agric. Exp. Sta. Res. Rep. 194, Bozeman.

Copeland, L. O. 1976. Principles of seed science and technology. Burgess Publ. Co., Minneapolis, MN.

Darwin, C. 1872 (Sixth edition). The origin of species. 1967. Macmillan Co., New York.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. pp. 307-323 In: S. T. A. Pickett and P. S. White (eds.). The ecology of natural disturbance and patch dynamics. Academic Press. Orlando, FL.

DePuit, E. J. 1980. Recent progress in mined land revegetation research in Montana. pp. 19(1)-19(24). In: Proceedings: Symposium on adequate reclamation of mined land, Billings, MT.

DePuit, E. J. 1982. Cool-season perennial grass establishment on northern great plains mined lands: status of current technology. pp. B1(1) - B1(24). In: F. F. Munshower and S. E. Fisher (eds.). Proceedings: Symposium on surface coal mining and reclamation in the Northern Great Plains. MT Agric. Exp. Sta. Res. Rep. 194, Bozeman.

DePuit, E. J. and J. G. Coenenberg. 1979. Responses of revegetated coal strip mine spoils to variable fertilization rates, longevity of fertilization program, and season of seeding. MT Agr. Exp. Sta. Res. Rep. 150, Bozeman.

DePuit, E. J. and E. F. Redente. 1986. Ecosystem dynamics on reconstructed semiarid lands. In: E. B. Allen (ed.). Symposium on reconstruction of disturbed arid ecosystems. 152nd Nat. Meeting, Amer. Assoc. Advan, Sci., Philadelphia, PA.

DePuit, E. J., J. G. Coenenberg and C. L. Skilbred. 1980. Establishment of diverse native plant communities on coal surface mined lands in Montana as influenced by seeding method, mixture and rate. Mt Agr. Exp. Sta. Res. Rep. 163, Bozeman.

DePuit, E. J., C. L. Skilbred and J. G. Coenenberg. 1982. Effects of two years of irrigation on revegetation of coal surface-mined land in southeastern Montana. J. Range Manage. 35:67-74.

Doerr, T. B., E. F. Redente, and T. E. Sievers. 1983. Effect of cultural practices of seeded plant communities on intensively disturbed soils. J. Range Manage. 36:423-428.

Edwards, G., and D. Walker. 1983. C_3, C_4: mechanisms, and cellular and environmental regulation, of photosynthesis. Univ. of CA Press. Berkeley.

Ellern, S. J., J. L. Harper, and G. R. Sager. 1970. A comparative study of the distribution of roots of Avena fatua and A. strigosa in mixed stands using a ^{14}C labelling technique. J. Ecol. 58:865-868.

Grime, J. P. 1979. Plant Strategies and Vegetation processes. John Wiley and Sons, New York.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52:107-145.

Harper, J. L. 1964. The nature and consequences of interference among plants. In: S. J. Geerts (ed.) Genetics Today. Proc. XI. Internat. Cong. Genet. 2:465-482.

Harper, J. L. 1977. Population Biology of Plants. Academic Press. London.

Huston, M. 1979. A general hypothesis of species diversity. Amer. Naturalist 113:81-101.

Hyder, D. N., A. C. Everson, and R. E. Bement. 1971. Seedling morphology and seedling failures with blue grama. J. Range Manage. 24:287-292.

Kemp, P. R., and G. J. Williams III. 1980. A physiological basis for niche separation between Agropyron smithii (C_3) and Bouteloua gracilis (C_4). Ecology 61:846-858.

Litav, M. and J. L. Harper. 1967. A method for studying the spatial relationship between the root systems of two neighbouring plants. Plant and Soil 26:389-392.

Monson, R. K., R. O. Littlejohn, Jr., and G. J. Williams. 1983. Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. Oecologia 58:43-51.

Risser, P. G. 1969. Competitive relationships among herbaceious plants and their influences on ecosystem function in grasslands. pp. 153-171. In: R. L. Dix and R. G. Beidleman. (eds.). The grassland ecosystem: a preliminary synthesis. Range Sci. Ser. No. 2, CO State Univ., Fort Collins.

Ross, M. A. and J. L. Harper. 1972. Occupation of biological space during seedling establishment. J. Ecol. 60:77-88.

Sabo, D. G., G. V. Johnson, W. C. Martin, and E. F. Aldon. 1979. Germination requirements of 19 species of arid land plants. USDA-FS Res. Paper RM-210.

Shannon, C. E. and W. Weaver. 1973. The
mathematical theory of communication. Univ.
Ill. Press. Urbana, IL.

Wasser, C. H. 1982. Ecology and culture of
selected species useful in revegetating
disturbed lands in the West. U.S.D.I., Fish
and Wildlife Serv., FWS/OBS-82/56, Fort
Collins, CO .

Welden, C. W. and C. W. Slauson. 1986. The
intensity of competition versus its importance:
an overlooked distinction and some
implications. Quart. Rev. Biol. 61:23-44.

White, P. S. and S. T. A. Pickett. 1985. Natural
disturbance and patch dynamics: an
introduction. p. 1-13. In: S. T. A. Pickett
and P. S. White (eds.). The ecology of natural
disturbance and patch dynamics. Academic Press.
Orlando, FL.

Wiens, J. A. 1977. On competition and variable
environments. Amer. Sci. 65:590-597.

Wilson, S. D. and P. A. Keddy. 1986. Species
competitive ability and position along a
natural stress/disturbance gradient. Ecol.
67:1236-1242.

Young, J. A. and R. A. Evans. 1982. Temperature
profiles for germination of cool season range
grasses. USDA-ARS ARR-W-27. 92p.

Young, S. A. and R. B. Rennick. 1982.
Establishment of seeded species on coal
minesoils following temporary irrigation. MT
Agr. Exp. Sta. Res. Rep. 200. Bozeman.

A STUDY OF FACTORS INFLUENCING SECONDARY SUCCESSION IN THE SAGEBRUSH [Artemisia spp. L.] TYPE

Richard E. Eckert, Jr.,[1] Frederick F. Peterson,[2] and Fay L. Emmerich[3]

ABSTRACT

This paper summarizes the effects of soil-surface type and precipitation probability on secondary succession. Surface types differ in microtopographic position; morphological, chemical, and physical properties; extent on different sites; and ability to support seedling emergence and plant establishment. Simulated precipitation of low probability can influence species response.

INTRODUCTION

Secondary succession depends on the periodic recruitment of new individuals of desirable species to replace plants of less desirable species. This can be a very slow process in arid or semiarid environments because weeds are not controlled, a seedbed is not prepared, seed quantity and quality are generally low, seed is not planted, and date of seeding is not optimum.

Land management agencies presently are monitoring trends in range condition and interpreting these trends based on management objectives. These objectives define the change in composition of key species that should occur for a given plant community in response to particular management strategies. If the probability of achieving these objectives is very low, one could confuse the improbability of a biological response to management with general fault of the management strategy. Understanding the reasons for, and the rate of, secondary succession is essential for the factual statement of management objectives and for the accurate interpretation of vegetation change. Such understanding can be used by land managers to: 1) identify soil limitations and potentials, 2) predict change in species composition, 3) determine why changes in species composition occurred or did not occur as predicted, 4) aid in the interpretation of changes in species composition due to grazing or other perturbations, and 5) extrapolate interpretations to similar ecological sites.

Rather than studying vegetation change over time, perhaps secondary succession could be simulated

through modeling techniques. Rangeland models can simulate increased forage production as management input increases and environmental conditions improve. Forage production stabilizes at some point because each ecological site has a finite production level based on the number of desirable forage plants and on the level of competition within the community. Further increases in production depend on increasing the composition of these species in the community, i.e., improving range condition through secondary succession.

Rangeland models dealing with perennial vegetation, however, cannot simulate secondary succession. The Simulation of Production and Utilization on Rangelands Model, SPUR, (Wight 1983) has a "Propagule" sub-component of the "Plant Growth" component, but SPUR cannot model the links between propagule production and recruitment of new plants through the processes of seed germination, seedling emergence, seedling survival, and plant establishment. The Annual Grassland Ecosystem Model, ELMAGE, (Pendleton et al. 1983) does have this capability because plants of annual species must regenerate each year in order to perpetuate the stand. The differences between regeneration requirements of annuals and perennials, in relation to yearly environment cycles, limit the use of ELMAGE for modeling secondary succession in the sagebrush [Artemisia spp. L.] ecosystem. Concepts from ELMAGE, however, may help develop a secondary succession capability for SPUR.

Development of a model for secondary succession requires knowledge about the functions of various factors influencing the establishment of perennial plants. Some of these factors are quantity and quality of seed of desirable, less desirable, and undesirable species; and the effects of season of emergence, level of competition, kind and amount of different soil surfaces, and amount and timing of precipitation on germination, emergence, and establishment requirements of these species. This paper will emphasize past and current research on the effects of soil-surface morphological type, and precipitation regime on secondary succession in the sagebrush type on crusting soils of Nevada's Humboldt loess belt.

SOIL-SURFACE MORPHOLOGICAL TYPES

Soils with so-called "vesicular A horizons", or "Av horizons", or patterned surfaces occur extensively in arid and semiarid regions. Vegetation generally occurs in coppices, bunches, or as separate individuals. The soil between plants is bare or only lichen covered. Where bare, the commonly crusted soil surface is cracked into polygons that have prominent vesicular pores in the upper few cm. Such features are the most commonly recognized criteria for these kinds of surface horizons (Lapham 1932; Springer 1958; Hillel 1959, 1960; Hugie and Passey 1964; Evaneri et al. 1974). In the Intermountain region, soils with vesicular

crusts are associated with northern-desert shrub plant communities that have sparse herbaceous cover in the understory. These soils commonly have A horizons that have been influenced by wind deposition of silt and very fine sand. This loess originated from sediments deposited in Pleistocene lakes and subsequently exposed to wind transport as the lakes dried (Young and Evans 1986). This area is informally called the Humboldt loess belt and comprises about 8 million hectares in central and northern Nevada and extends into southeastern Oregon, southern Idaho, and western Utah. The loess cap is shallow, roughly 10-30 cm thick, and partially mixed into underlying gravelly and cobbly alluvium or colluvium. The loess was deposited rapidly enough, or thickly enough, or continuously enough that rock fragments in the underlying material are mostly buried. Soil surfaces have only scattered pebbles; desert pavement is uncommon.

Hugie and Passey (1964) found that polygonally-patterned soils in Nevada, Idaho, and Utah have silt loam, very fine sandy loam, or silty clay loam surface textures. Polygonal surface patterns occur only on bare soil; not under stones, cobbles, or moderately thick mulch. These patterns are most common on flat or nearly level landscapes, though they do occur on flattish, small terraces on steep slopes. These patterns are most prominent after the surface has dried in late spring or early summer. Polygonal cracking was attributed to freezing, thawing, and desiccation-shrinkage. These workers suggested that the characteristic fine platyness of polygons is due to ice-lens formation, and that the coarse vesicular porosity is due to expansion of trapped gas on warming. They did not emphasize the relation of surface patterns to the microtopography under and between plants. Schlatterer (1968) called the microrelief under and between shrubs "mound" and "intermound", respectively. The mounds of trapped, wind-blown soil and litter under shrubs more commonly have been called "coppice dunes" and the areas between them are called "dune interspaces" (Melton 1940; Stuart et al. 1971, 1973; Blackburn 1975). Crusted soils with vesicular porosity can negatively affect range improvement and management by acting as a mechanical barrier to seedling emergence (Taylor 1971) and by decreasing water infiltration and increasing soil erosion (Blackburn 1975).

Our field observations suggested further studies to clarify the nature of these soil surfaces and their role in the function of rangeland ecosystems. These studies include: 1) detailed description of soil surfaces with different patterns, 2) relating different soil-surface morphological types to microtopography and vegetation, 3) determining the ecological significance of various soil-surface types, and 4) determining the influence of soil surfaces on secondary succession.

Characteristics of Soil Surfaces

Kinds of Soils and Horizons Identification

The 23 study sites that have been partly reported in previous publications are considered here (Wood 1976; Wood et al. 1978, 1982; Eckert et al. 1977, 1986a, 1986b; Stephens 1980; and Belton[4]). For these studies, soils were described by standard procedures (USDA 1951) and identified at the Family level of soil taxonomy (USDA 1975). Particle size classes for the Family control sections are fine, fine-loamy, and coarse-loamy. All soils have mesic soil temperature regimes. All are in xerollic subgroups of Argids or Orthids (Table 1). These soils support Wyoming big sagebrush [Artemisia tridentata ssp. wyomingensis Beetle and Young] and basin big sagebrush [A. tridentata ssp. tridentata] vegetation types that occur on fan piedmonts and basin floors. The relations reported here cannot be extrapolated to the more moist Xerolls at higher elevations or to the warm, desert-paved Aridisols to the south.

Horizon identifications in this paper follow current, standard soil-survey notation (Guthrie and Witte 1982) with one exception. The informal notation "Av" is used for A horizons that have a polygonally-crusted, coarsely-vesicular upper part; the notation "Alv" is used for the upper subhorizon. The postscript "v" is not official, but is commonly used. Readers familiar with older horizon notation should note that an "A2" notation no longer means "eluviated", rather it merely means the second subhorizon of an A horizon. An eluviated horizon is now noted as an E horizon.

In standard soil survey reports, soil-surface morphological types are not reported. Rather, the morphology of the A horizon is inferred by the phase of a soil series or family that is used to identify the soil(s) in a map unit. Any soil profile description for the components of a map unit will give either the general morphology for the A horizon, or if a detailed profile description is made, the narrative will be for the A horizon morphology only at the point where the profile was described. This point most likely will be in the interspace between shrubs. No estimate of the proportions of soil-surface types is given in soil survey reports, but one can readily estimate this by line intercept measurements of the extent of microtopographic positions that are associated with various surface types.

Microtopographic Positions

The four soil-surface morphological types found on 23 study sites are closely and genetically associated with specific microtopographic positions (Table 2). The name for the "coppice

---

[4]Unpublished data, USDA-ARS, Reno, NV.

Table 1. Location, soil Family identification, and type of study on 23 sites in central and northern Nevada.

Location	Soil Family Identification	Type of study
Crowley Creek		
1	Fine-montmorillonitic, mesic Xerollic Durargid	Ecological and natural population
2	Fine-loamy, mixed, mesic Xerollic Durorthid	"
3	Coarse-loamy, mixed, mesic Xerollic Durorthid	"
4	Coarse-loamy, mixed, mesic Xerollic Durorthid	" \
5	Coarse-loamy, mixed, mesic Xerollic Durorthid	"
6	Coarse-loamy, mixed, mesic Xerollic Durorthid	"
7	Coarse-loamy, mixed, mesic Xerollic Durorthid	"
Sheep Creek		
1	Fine-loamy, mixed, mesic Xerollic Durargid	"
2	Coarse-loamy, mixed, mesic Xerollic Camborthid	"
3	Fine-montmorillonitic, mesic Xerollic Durargid	"
4	Fine-montmorillonitic, mesic Xerollic Durargid	"
5	Fine-montmorillonitic, mesic Xerollic Durargid	"
6	Fine-loamy, mixed, mesic Xerollic Durargid	"
7	Coarse-loamy, mixed, mesic Xerollic Durorthid	"
8	Coarse-loamy, mixed, mesic Xerollic Durorthid	"
9	Fine-montmorillonitic, mesic Xerollic Haplargid	"
Dinner Station 2	Fine-montmorillonitic, mesic Durixerollic Haplargid	Cattle trampling
McClelland Creek	Fine-montmorillonitic, mesic Xerollic Haplargid	"
Coils Creek	Fine-montmorillonitic, mesic Abruptic Xerollic Durargid	Seeding and simulated trampling
Paradise Valley	Fine-loamy, mixed, mesic Abruptic Xerollic Durargid	"
Jiggs	Fine-loamy, mixed, mesic Xerollic Durargid	"
Panther Canyon	Fine-loamy, mixed, mesic Xerollic Durorthid	"
Dinner Station I	Fine-montmorillonitic, mesic Durixerollic Haplargid	"

dune" position of earlier work is abbreviated here as "coppice". The "dune interspace" of earlier work, abbreviated here as "interspace", is subdivided into "coppice bench", "intercoppice microplain", and "playette" positions. Soil-surface types associated with these four microtopographic positions are named, respectively, by Roman numerals: I, II, II, and IV. Microtopographic positions and related soil-surface types must be named separately because different surface types can occur on the same microtopographic position on other landscapes.

Morphology of Soil-Surface Types

Soil-surface types are identified by their microtopographic position; diameter of polygons; flatness, convexity, or pinnacled nature of polygon tops; width and shape of cracks between polygons; and internal structure of polygons. Figure 1 shows three soil-surface types under field conditions. Figure 2 is a schematic diagram of polygon morphology and microtopographic position where the four surface types most commonly occur. Surface polygons, named after their outlines at the soil surface, actually are the tops of squat, very coarse prisms that extend down through the entire A horizon, and in some cases, into the B horizon. The process of recurrent swelling and shrinking forms the vertical crack patterns that are the prism faces. The faces (i.e., cracks) are prominent in the crusted A1 subhorizon and can be traced through the A2 subhorizon, but are difficult to distinguish in root-proliferated and litter covered surfaces. The cracks are either wide or narrow at the top, depending on soil-surface type, but in all types narrow rapidly, within 1-2 cm depth, to <1 mm wide. These vertical cracks between prisms are preferred channels for root growth and water infiltration. The major morphological and behavioral contrasts of soil-surface types are between the non-crusted A1 subhorizon of Type I and II surfaces and the crusted A1v subhorizon of the Type III and IV surfaces. The A2 subhorizon under all surfaces is quite similar; it is slightly hard, friable, and compound finely platy and subangular blocky. The horizontal cracks between platy peds are preferred channels for root growth, but they restrict or slow water infiltration. The A1 subhorizon of Type I and II surfaces is not coarsely vesicular; if finely vesicular, it is not significantly crusted. The A1v subhorizon of the Type III and IV surfaces is always crusted and coarsely vesicular if not recently trampled.

The Type I surface forms on shrub coppices (shrub-Type I) or bunchgrass coppices (bunchgrass-Type I). The 5-10 cm diameter polygons are convex-topped and separated by about 2 cm wide by 1-2 cm deep "trench-cracks", abbreviated here as "trenches", that rapidly narrow at the bottom. The trenches are not visible because they are filled with litter and the entire soil surface is covered with litter, lichen, or moss [Tortula ruralis (Hedw.) Gaertn.,

Table 2. Soil-surface morphological types, their microtopographic positions, and description of microtopographic position.

Soil-surface morphological type	Microtopographic position	Description of microtopographic position and clues for identification
I	Coppice	A semi-conical heap of eolian and animal-burrow-spoil material under shrubs or bunchgrass; litter covered; highest microtopographic position.
II	Coppice bench	Flattish or glently-sloping area at margin of a coppice, or a former coppice now lacking a major live shrub and somewhat eroded or slumped, or on the intercoppice microplain with a thick A horizon; no litter cover; next highest to the coppice, higher than any adjacent intercoppice microplain or playette (absent in a few situations).
III	Intercoppice microplain	The gentle slope from a coppice or coppice bench down to a playette or to a micro-drainageway; next lower than the coppice bench (absent in a few situations).
IV	Playette	The flat or slightly-depressed area at the lowest local microtopographic position; surrounded by intercoppice microplains, coppice benches, and coppices; collects shallow standing water after heavy storms or snowmelts and may overflow to a next-lower playette or micro-drainageway on sloping soils (absent or infrequent in many situations).
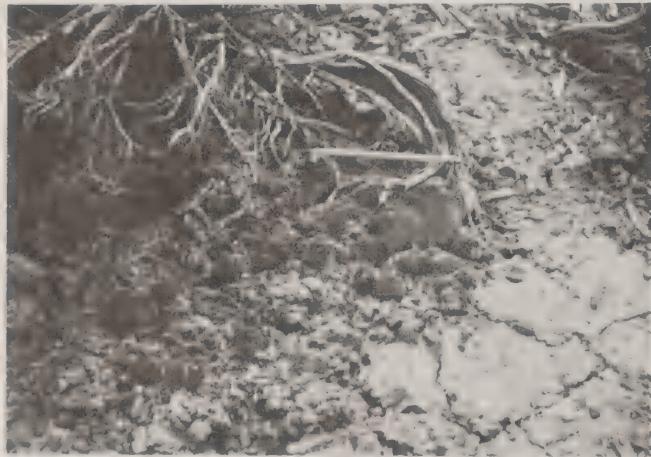
Figure 1. Example of soil-surface types: Type I under the shrub is covered with moss and litter; Type II in the lower left of photograph has small, pinnacled polygons separated by trench-cracks and stabilized by cryptogamic crust; and Type III in lower right of photograph has large, flat polygons separated by narrow cracks.

Meyer and Scherb.] where not trampled. The polygons are not crusted, are only very slightly hard, have a weak to moderate very fine subangular blocky structure, and absorb water rapidly. The area of Type I surface commonly is somewhat larger than the shrub-canopy cover or the bunchgrass basal-area cover and forms a semicircle under single shrubs or grass bunches, or a lobate area up to a few m long when shrubs or grass bunches are closely grouped.

The Type II surface occurs most commonly as discontinuous, lobate, 0.3-1.5 m wide margins around coppices, or on 0.5-3 m wide coppice benches, or on microplains with an A horizon that is coarse-loamy, thicker than about 15-20 cm, and has not been trampled repeatedly. The 7-15 cm diameter polygons are either prominently convex-topped, or more commonly are frost-heaved into irregular pinnacles about 1-3 cm high by 2-3 cm diameter. Prominent, 2 cm wide by 1-2 cm deep trenches separate polygons. The surface is partly lichen covered or bare, depending on recentness of trampling. Where bare, the mineral surface is smooth, as if crusted, but the surface is fragile and readily accepts water. Internally, Type II polygons are only very slightly hard and are massive or very weakly platy and subangular blocky.
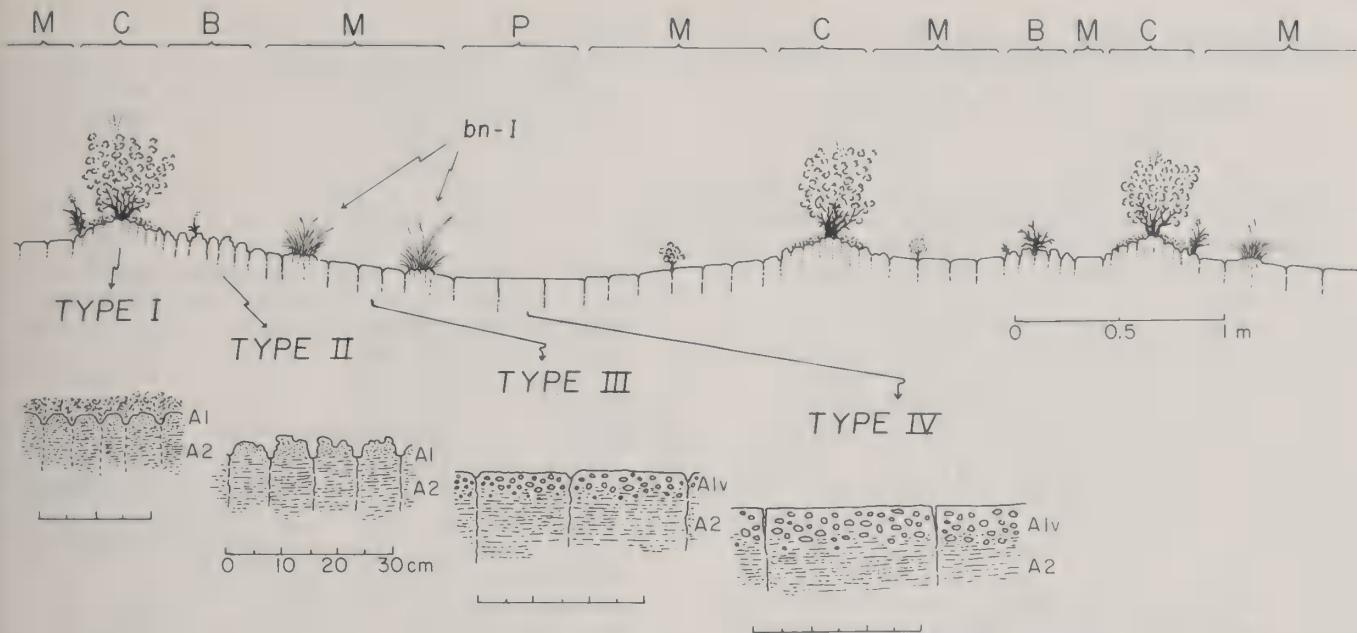
Figure 2. Schematic cross-sectional diagram of the microtopographic positions of four soil-surface types, including bunchgrass-Type I (bn-I) associated with gently sloping, shallowly loess-mantled xerollic Argids and Orthids of the Humboldt loess belt. Microtopographic positions are: C = coppice, B = coppice bench, M = intercoppice microplain, P = playette. Vertical scale is somewhat exaggerated. Type I is litter covered. Circles indicate vesicles in the crust (Alv).

The Type III surface forms on intercoppice microplains. The prominent polygons are flat-topped, about 13-26 cm diameter, and separated by relatively narrow trench cracks, abbreviated here as "cracks", that are 1 cm wide and 1 cm deep. The polygon top is a 1-4 cm thick, durable, vesicular crust. Below the crust the polygons are compound fine platy and very fine subangular blocky. Depending on recentness of trampling, the surface is bare or partly lichen covered and pebbles may have collected in the cracks around polygons. The microplains are gentle, 0.2-5 m wide slopes around coppices or coppice benches. Then they are almost flat for 0.3-2 m reaches, forming indistinct steps leading down to playettes or to minuscule drainageways.

The Type IV surface forms on semicircular or elongated playettes that are from 0.5-5 m wide. They are barren, notably smooth, and light colored. The flat-topped, 20-36 cm diameter polygons are the largest of all, but are separated by the narrowest, most sharply angular-shouldered cracks that are less than 1 cm wide. The crust is 4-8 cm thick, coarsely vesicular, and massive in its upper part, grading to platy with depth. This surface type was not included in subsequent studies because of its limited extent on the 23 sites.

Genesis of the Soil-Surface Types

The diagnostic morphology of each soil-surface type is the apparent result of primarily 1) the dispersibility, or propensity to slake, of the soil material, 2) the lack of, or frequency and depth of saturation of the A1 subhorizon, and secondarily 3) depth to a slowly pervious B

horizon. Coppices are formed at least partly by accumulations of recent wind-blown material under a shrub or grass bunch. Evidence is the occurrence of shrub or grass seedlings in Type II, III, or IV polygon cracks without coppices, occurrence of intermediate-size shrubs and grass bunches with small coppices, and the association of the largest coppices with the largest, oldest shrub and grass plants. Incorporation of litter and root residues concurrently with accumulation of relatively sandy eolian material results in formation of humus and a moderate, very fine, subangular blocky structure that does not slake readily and does not form a crust after wetting and drying. Coppice benches are old coppices. Litter and mulch are absent and dead shrubs may or may not be present. The A horizon has retained much of the humus and structure of the parent coppice. The low-clay, silty and fine-sandy surficial soil material of the Type III and IV surfaces is relatively light-colored, low in humus, and slakes readily when wet and dries to a massive crust after saturation and drying.

During heavy rain storms or snowmelt, water does not stand on coppices or coppice benches and is very seldom seen running across them. Water runs slowly over the microplains and may pond briefly. During major snowmelts, thin sheets of ice can form at night on flattish microplains. Water ponds on the playettes after only moderate rain storms and stands longest there during snowmelt. The thickest, most coarsely-vesicular crusts occur on playettes, where surficial saturation is the most frequent and longest lasting. Thinner crusts are found on microplains, where surficial saturation should be less frequent, and insignificant or no crusting occurs on coppices and coppice benches. For

ecological interpretation, it is important to note that a crust exists only when the surficial layer is dry. When moist, the surface layer has little or no strength and will not prevent seedling emergence.

Given rapid enough water addition to sheet-flood or pond, soil hydraulic conductivity determines the rate and depth of surficial saturation. Slaking very fine sandy loams and silt loams have such critically low conductivity. Two other morphological features probably contribute to low surficial water conductivity. 1) Water percolating by unsaturated flow is markedly retarded when it passes from a finely porous layer to a more coarsely porous layer (Miller 1973). The platy structure of the lower Alv and A2 subhorizons interposes a horizontal macroporosity that could favor surficial saturation. Miller (1971) suggested that growth of coarse vesicles should also decrease the saturated conductivity of the Alv subhorizon because vesicles remain air filled and decrease the cross-sectional area of water-filled, water conducting micropores. However, he found that infiltration rate actually increased with successive saturation events in field-scale trials on plowed, then irrigated, vesicularly crusting soils. One obvious explanation is that the cracks between the shrinkage-polygons, which form concurrently with vesicularity, should add significant macroporosity. 2) Water penetration also is retarded by underlying, slowly pervious argillic horizons. After summer storms, Type III and IV surfaces can be temporarily and shallowly ponded, and saturated down to a shallow (10-15 cm deep) argillic horizon. Adjacent Type I and II surfaces are more deeply wetted, and are neither ponded nor saturated. Shallow argillic horizons may determine the occurrence of many Type III and IV surfaces.

Crusting is the direct result of slaking soil material being saturated and then drying; the greater the degree of saturation and, to some extent, the slower the drying the stronger the crust (Hillel 1960). The slaking, or dispersible character of soil material allows skeletal grains to rearrange into maximum packing densities and plasma grains (clay) to migrate to and deposit at the grain-contact vertices as the reversible cement that hardens the crust as it dries. Vesicular pores form and enlarge during recurrent saturations of crusting material because the skeletal grains are free to rearrange and allow entrapped air to migrate from smaller to larger air-filled pores, as can be predicted from capillarity principles (Miller 1971). The largest shrinkage-polygons form in the least structured, i.e., most massive and compact soils that are most apt to be surficially saturated. The vesicularly-crusted Type III and IV surfaces would seem to be a consequence of their slaking character and exposure to recurrent, brief periods of saturation then desiccation. Their large polygon size also fits this interpretation. The non-crusted Type I and II surfaces have well-structured material that is not apt to slake and probably is seldom, if ever, surficially saturated. The pinnacling of the

Type II surface is probably the result of frost heaving. Pinnacles have been observed to form over winter on freely-drained, silty soils in this region. Cryptogams apparently stabilize the pinnacles.

Trampling and Surface Reformation

Following crushing and powdering of a soil surface, such as by livestock trampling, each surface type seems to reform if its microtopographic position has not been obliterated. In all cases, with the first few wettings the powdered Alv subhorizon slakes to a massive, nonvesicular crust with relatively large, flat, angular-shoulder polygons. With successive saturation-drying cycles, the Type IV surface reforms its coarse vesicles and narrow cracks. The Type III surface regains coarse vesicularity and polygon shoulders round to the pre-existing condition. The powdered Al subhorizon of the Type II surface reforms into small polygons with merely rounded cracks and only marginal, small pinnacles. Finally the cracks become trenched, the entire polygon top becomes pinnacled, and the initially massive surface regains its platyness and friability. Trampled Type I surface probably first converts to a Type II surface and then, as litter collects, back to a Type I surface.

Vegetation Patterns on the Soil-Surface Types

The shrub-Type I surface regularly supports shrubs; occasionally the plant is dead but the coppice is still intact. Bunchgrass may or may not occur under or to the side of the shrub, depending on range condition. The interior of the coppice is covered at least partially with litter, otherwise it is mostly moss and lichen covered. Coppice margins commonly show bare soil and prominent, frost-heaved pinnacles with Sandberg bluegrass [Poa sandbergii Vasey] on top of some of the pinnacles. A bunchgrass-Type I surface can occur at the base of a perennial bunchgrass within the Type II, III, or IV matrix.

The Type II surface is well or poorly vegetated, depending on range condition. Bunchgrass, shrub, and forb plants occur in or near a trench. On low condition sites, cheatgrass [Bromus tectorum L.] commonly grows out of the trenches and covers the small polygons with litter. Cryptogams stabilize the surface on sites protected from trampling for long periods.

The Type III surface is mostly barren. Widely spaced phlox [Phlox spp. L.) and brush plants grow from the cracks and a few Sandberg bluegrass or squirreltail [Sitanion hystrix (Nutt.) J.G. Sm.] plants grow in or beside cracks. Cryptogams can cover the entire Type III surface where it has been very well protected from trampling. Type IV surface is almost always barren except for partial lichen cover around polygon margins on sites long protected from trampling.

Table 3. Organic carbon, bulk density, and modulus of rupture characteristics for Type I and Type III surface soils on four sites in central and northern Nevada.[1]

Site	Soil-surface type	Organic carbon	Bulk density	Modulus of rupture
		(%)	(g/cc)	(N)
Lower Coils Creek	Type I	2.1	0.90	0.18
	Type III	0.9	1.42	0.76
Upper Coils Creek	Type I	3.4	0.83	0.00
	Type III	1.2	1.25	0.61
Panther Canyon	Type I	2.3	0.87	0.05
	Type III	0.7	1.25	0.84
Paradise Valley	Type I	2.0	0.90	0.00
	Type III	0.3	1.36	0.56

[1]From: Wood, M.K. 1976.

Soil Chemical and Physical Properties

Wood (1976), Eckert et al., (1977), and Wood et al. (1978) described some of the chemical and physical characteristics of Type I and III surfaces on four sites in central and northern Nevada (Table 3). The Type I soil is much higher in organic carbon and is not as dense or hard as is the Type III soil. Belton[5] found that for 16 sites in northcentral Nevada, the organic carbon content of Type I surface averages 1.8% compared to 1.5% for Type II surface and 0.6% for Type III surface. Bulk density of Type II surface is 1.02 g/cc compared to 1.10 g/cc for Type III surface. The organic carbon content of Type II and III soil surfaces on three ecological sites in northeastern Nevada is, respectively, 2.4 and 0.4% for the Loamy 8-10" site, 2.7 and 1.1% for the Loamy 10-12" site, and 2.3 and 1.0% for the Claypan 10-12" site (Eckert[6]).

Influence of Soil-Surface Type on Seedling Emergence

Wood (1976) and Wood et al. (1978) postulated that the surface horizon should become hard and vesicular when rangelands that are in good condition, but have a soil surface with the potential to become vesicular, are overgrazed and trampled to the extent that herbaceous vegetation in the interspaces between shrubs is destroyed and the surface horizon is pulverized repeatedly. The organic matter in these interspaces should be reduced by oxidation. Without additions of litter each year and with continued surface disturbance, crusting and vesicular porosity should increase as should stress on seedlings. This effect was evaluated for crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Schult.] and squirreltail during emergence from Type I and III surfaces watered to saturation at 3 and 6 day intervals. Total emergence was determined after 3 weeks and each seed and seedling was given a stress rating.

Significantly more crested wheatgrass and squirreltail seedlings emerged from Type I soil than from Type III soil regardless of the watering treatment (Table 4). Both watering treatments resulted in good emergence of both species from Type I soil. However, neither watering treatment was sufficient to moisten and soften Type III soil crust enough to permit adequate emergence of either species.

Crested wheatgrass and squirreltail exhibited least seedling stress in Type I soil and there was no significant difference due to watering treatment on stress of either species in this soil (Table 5). Seedlings of both species in Type III soil watered every 3 days showed moderate to heavy stress whereas plants watered every 6 days showed heavy and extreme stress and some seeds did not germinate. Watering every 3 days reduced stress symptoms for both species in Type III soil (Table 5), but did not increase emergence (Table 4). Squirreltail stress values were generally higher than those for crested wheatgrass regardless of soil or watering treatments.

The effect of a hard crust on seedling emergence has not been quantified for native and exotic species generally adapted to arid and semiarid rangelands. Tall wheatgrass [Agropyron elongatum (Host) Beauv.], a relatively large-seeded species closely related to those used in range seeding, had a maximum emergence force of 0.06 newtons (Gifford and Thran 1969). Based on this information, tall wheatgrass could not emerge through crusts formed by one of the Type I and all of the Type III surfaces listed in Table 3. This comparison suggests that emergence of exotic grasses with small seeds, or of native grasses with low seedling vigor, should be quite low in hard-crusted soil surfaces. Due to the inability of seedlings to emerge under these conditions, areas of well developed soil crusts commonly are devoid of vegetation. The few plants present are usually annual weeds in cracks between polygons.

[5]Unpublished data, USDA-ARS, Reno, NV.
[6]Unpublished data, USDA-ARS, Reno, NV.

Table 4. Mean emergence after 3 weeks of crested wheatgrass and squirreltail seedlings in Type I and Type III surface soils watered every 3 or 6 days.[1]

| Soil surface | Watering cycle | Emergence | |
		Crested wheatgrass	Squirreltail
	(days)	(%)	(%)
Type I	3	88 a[2]	58 a
	6	80 a	45 a
Type III	3	15 b	5 b
	6	3 b	0 b

[1]From: Wood, et al. 1978.
[2]Means within a column with different letters differ (P < 0.05).

Table 5. Mean stress symptoms after 3 weeks exhibited by crested wheatgrass and squirreltail seeds and seedlings in Type I and Type III surface soils watered every 3 or 6 days.[1]

| Soil surface | Watering cycle | Stress rating[2] | |
		Crested wheatgrass	Squirreltail
	(days)		
Type I	3	1.6 c[3]	2.3 c
	6	1.8 c	2.4 c
Type III	3	3.8 b	4.2 b
	6	4.7 a	5.6 a

[1]From: Wood, M.K. 1976.
[2]Stress ratings:
  1. No visual stress - root and coleoptile development normal.
  2. Slight stress - coleoptile length greater than 2.5 cm but coleoptile or roots are slightly wavy.
  3. Moderate stress - coleoptile length less than 2.5 cm but greater than 1 mm. Coleoptile and roots with prominent wavy shape.
  4. Heavy stress - coleoptile length less than 2.5 cm but greater than 1 mm. Coleoptile or root growth less than for ratings above.
  5. Extreme stress - germination started but stopped immediately. Coleoptile length less than 1 mm.
  6. Failure - seed did not germinate or coleoptile did not break the seed coat.
[3]Means within a column followed by different letters differ (P < 0.05).

ECOLOGICAL SIGNIFICANCE OF SOIL-SURFACE TYPES

Relation to Range Condition

Observations made during the course of descriptive soil studies suggested that areal coverage of soil-surface types varied with ecological-range condition of the site. The bunchgrass-Type I and Type II surfaces appeared to be more prevalent on sites in late-seral range condition with the Type III surface more prevalent on sites in early-seral range condition. Eckert et al. (1986a) conducted a study to define this relationship on 16 sites in northcentral Nevada (Table 1).

The inference technique (Tueller and Blackburn 1974) was used to choose study areas. This technique assumes that it is possible to select study areas with similar enough soils, elevation, slope, and exposure so that site potential is similar. Soil properties and remnant vegetation suggested that all sites have the potential to produce a similar kind and amount of vegetation dominated by Wyoming big sagebrush, the principal increaser species in the overstory, and by Thurber needlegrass [Stipa thurberiana Piper], the principal decreaser species in the understory. Vegetation on each study area was stratified on the basis of abundance of Thurber needlegrass. Within each stratum, a homogenous stand of vegetation was located and canopy cover of shrubs, areal cover of soil-surface types, and basal-area cover of bunchgrasses were determined.

Vegetation on each site was placed in one of four ecological-range condition classes based on differences in the basal-area cover of Thurber needlegrass (Table 6). Two sites are considered to have the potential-natural community (PNC); four sites late-seral condition; four sites mid-seral condition; and six sites early-seral condition. This classification was based on the fact that mean basal area of Thurber needlegrass (2.7%) on sites in late-seral condition is similar to that on high condition sites representing the Wyoming big sagebrush-Thurber needlegrass habitat type in southern Idaho (personal communication, M. Hironaka). The Nevada sites with a greater mean basal cover of needlegrass (4.6%) may represent an even higher condition class than that described in Idaho. The range condition terminology used is that proposed by the Range Inventory Standardization Committee (1983). PNC, and late-, mid-, and early-seral classes are equivalent to the excellent, good, fair, and poor classes, respectively, as defined by the USDA (1976) and used to compare present vegetation with potential vegetation.

The proportion of each soil-surface type varies with ecological-range condition (Table 6). Total cover of Type I surface is related to the cover of shrub-Type I and bunchgrass-Type I surfaces and is greatest on sites in either early- or late-seral condition. The cover of bunchgrass-Type I surface is from three to nine times greater on sites with PNC than on sites in lower

Table 6. Mean vegetation and soil-surface characteristics associated with four range condition classes on sites in northern Nevada with potential vegetation of Wyoming big sagebrush and Thurber needle-grass.

Ecological-range condition and number of sites	Vegetation characteristics (Cover)				Soil-surface characteristics (Surface cover)				
	Canopy, big sagebrush	Basal, decreaser grasses	Basal increaser grasses	Basal, total perennial grasses	Shrub-Type I	Bunchgrass-Type I	Total-Type I	Type II	Type III
	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Potential natural community (2)	16 b[1]	4.6 a	2.6 a	7.2 a	21 b	9 a	30 ab	61 a	9 c
Late-seral (4)	18 b	2.7 b	3.3 a	6.0 ab	32 a	3 b	35 a	44 b	21 b
Mid-seral (4)	22 ab	1.0 c	3.3 a	4.3 b	29 a	1 bc	30 b	45 b	25 b
Early-seral (6)	26 a	T[2]d	2.1 a	2.2 c	33 a	T c	33 a	32 c	35 a

[1] Means within a column followed by different letters differ (P < 0.05).
[2] T = < 1% basal area or soil-surface cover.

seral stages. The basal area of decreaser grasses and bunchgrass-Type I surface varies concomitantly with range condition, but basal area of increaser grasses does not vary with range condition. This response suggests that formation of a bunchgrass-Type I surface is more dependent on the presence of decreaser grasses than on increaser grasses. Longevity of decreaser grasses, amount of litter deposited, litter quality, and root characteristics may be responsible for development and maintenance of a bunchgrass-Type I surface.

Bunchgrass-Type I, Type II, and Type III surfaces vary more with range condition than do shrub-Type I or total-Type I surfaces (Table 6). Basal cover of bunchgrass in the interspaces among shrubs is greater on sites in PNC and in late-seral condition than on sites in lower range condition. Since each bunchgrass plant has a Type I surface at its base, this bunchgrass-Type I surface is more frequent and extensive in the shrub interspaces of high condition sites than of low condition sites. Also on high condition sites, the Type II surface forms patchy, cryptogam-stabilized areas on the microplains in shrub interspaces. Less of the Type II surface occurs on the microplain of low condition sites.

Based on their data, the authors proposed a scenario of how change in the proportions of soil-surface types with change in range condition might affect the hydrologic and natural revegetation characteristics of a site. Sites in high range condition have a greater cover of bunchgrass-Type I and Type II surfaces than do sites in low range condition. Because these two surfaces have fine-subangular blocky or weak platy structures and few, small vesicular pores, hydrologic characteristics should be favorable (Loope and Gifford 1972, Blackburn 1975). The common depression microsites and friable soil of these surfaces may also favor natural revegetation (Eckert et al. 1978). Also, since these two surfaces occur on the microplains in

shrub interspaces, beneficial hydrologic and revegetation effects are spread across the site. Sites in high range condition also have a small coverage of Type III surface with its unfavorable hydrologic (Blackburn 1975) and revegetation (Eckert et al 1978, Wood et al. 1978) properties that are due to crusts with a smooth surface, massive structure, and vesicular porosity. Sites in low range condition have less cover of bunchgrass-Type I surface because of the loss of decreaser grasses and less cover of Type II surface because of physical destruction by livestock hoof action (Anderson et al. 1982). With reduced cover of these two surfaces, the proportion of Type III surface is greater and fewer microsites are available for rapid infiltration of water or for natural revegetation.

Relation to Natural Revegetation

Harper et al. (1965) and Evans and Young (1972) have described the widely contrasting environmental conditions for seed germination and establishment of annual plants in microsites created by various kinds of soil-surface microrelief. Young et al. (1969) found that the number of favorable microsites, or "safe sites", on a soil surface determines the maximum possible population density of cheatgrass. Evans et al. (1970) and Evans and Young (1970) quantified temperature and soil moisture conditions in safe sites created by plant litter and by mechanical drilling and furrowing. They found that depressions in a rough soil surface favor seed germination and seedling establishment.

The relationship between surface microsites and germination and establishment of annual species also could have application to natural revegetation by perennial species and either secondary succession or retrogression. The only previous research on this subject was conducted

Table 7. Mean density of seedlings and young plants on each microsite of Type II and III soil surfaces in June at 12 locations.

Soil-surface type	Microsite	All species	All forbs	Big sagebrush	Sandberg bluegrass	Microsteris
				No./m^2		
II	Pinnacle	54 b[1]	41 b	8 a	3 b	30 b
	Trench	151 a[2]	114 a	8 a	4 a	42 a
	Combined	205 A[2]	155 A	16 B	7 A	72 A
III	Polygon	56 b	30 b	20 a	2 b	22 a
	Crack	74 a	44 a	13 b	3 a	24 a
	Combined	130 B	74 B	33 A	5 A	46 B

[1] Means for each species or species group for each microsite within a soil-surface type followed by different small letters differ (P < 0.05).
[2] Means for species or species group for each soil-surface type followed by different capital letters differ (P < 0.05).

by Hugie and Passey (1964) and Schlatterer (1968) who found that seedlings of perennial grasses and forbs emerged and became established almost exclusively in certain soil-surfaces. Species response to cracks, protrusions, and flat spots on surface soils of the Humboldt loess belt was determined in three studies by Stephens (1980) and Eckert et al. (1986b): 1) the relation between kinds of microsites present on various soil-surface types and existing natural plant populations, 2) the influence of intensity of trampling by cattle on seedling emergence from various microsites, and 3) an evaluation of seedling emergence and survival in relation to microsite and simulated trampling.

Natural Plant Populations

A study of the influence of soil-surface microsites on existing natural plant populations was made on 16 sites in the Crowley Creek and Sheep Creek areas of northcentral Nevada (Table 1). Potential vegetation on all sites is Wyoming big sagebrush and Thurber needlegrass. Estimated annual precipitation for each site is about 200 to 250 mm. Precipitation patterns probably resulted in at least average seedling emergence in the spring and survival of these seedlings until time of sampling. Density of seedlings and young plants on pinnacle or in trench microsites of the Type II surface and on polygon or in crack microsites of the Type III surface was determined.

Average densities of seedlings and young plants for all species, all forbs and microsteris [Microsteris gracilis (Hook.) Greene] were significantly greater: 1) on the Type II surface than on the Type III surface, 2) in trenches than on pinnacles of the Type II surface, and 3) in

cracks than on polygons of the Type III surface (Table 7). Sandberg bluegrass followed the same trend except that plant densities were similar on the Type II and III surfaces. Big sagebrush was the exception with 1) significantly more plants on the Type III surface than on the Type II surface, 2) similar densities in trenches and on pinnacles of the Type II surface, and 3) more plants on polygons than in cracks of the Type III surface. Of the less common species, Thurber needlegrass density was similar on pinnacles and polygons but significantly more plants were found in trenches of the Type II surface than in cracks of the Type III surface and in trenches and cracks than on pinnacles and polygons. For example, average plant density was 1, 1, 7, and 12 plants/m^2 on polygons and pinnacles and in cracks and trenches, respectively.

Most of the study sites are in early- to mid-seral range condition and most of the herbaceous vegetation grows on the Type II surface. Small-seeded species appear to find an adequate safe site on the pinnacle microsite. Larger seeds of annual and perennial grasses, perennial forbs, and microsteris probably fall in trenches of the Type II surface and may be covered with the friable soil on this surface by trampling. Propagules disseminated by wind, such as those of squirreltail, composite forbs, and composite shrubs tend to blow across the soil surface. Seed may lodge in trenches of the Type II surface where soil is friable. Seed may also lodge in the narrow cracks of the Type III surface and have poor seed-soil contact, or cracks may fill with soil due to trampling. Seed may also remain on the polygon surface or be mixed into the soil by hoof action. If a durable crust forms after wetting and drying cycles, emergence in cracks and on the polygon surface could be restricted. Although many seedlings may die after sampling,

Table 8. Mean density of big sagebrush, perennial bunchgrass, and perennial and annual forb seedlings in trench and on pinnacle microsites of the Type II surface and in crack and on polygon microsites of the Type III surface in June at the Dinner Station 2 site. The sites had been protected from trampling or moderately trampled for many years before sampling.

Species	Type II		Type III		Type II		Type III	
	Trench	Pinnacle	Crack	Polygon	Trench	Pinnacle	Crack	Polygon
	1-yr protection				Moderate trampling			
				No./9 m^2				
Shrub								
Big sagebrush	25 a[1]	7*[2]	56 a*	29*	15	16	4	61 a
Perennial grass								
Sandberg bluegrass	35 a*	2*	17 a*	2*	90 a	24	57	131 a
Squirreltail	52 a*	2*	12 a*	4*	85 a	26	38 a	28
Perennial forb								
Desert phlox	89 a*	7	120 a*	5	342 a	13	196 a	24
Wild onion	59 a*	14	51*	49	12	18	15	20
Hawksbeard	38 a*	2	56 a*	12	21 a	7	13 a	7
Biscuitroot	47 a*	6	52 a*	14	26 a	7	25 a	9
Annual forb								
Little-flowered collinsia	584 a*	80*	245 a*	98*	342 a	139	163	164
Microsteris	182 a*	46*	200 a*	159*	103 a	28	61	69

[1] Means within a trampling treatment between microsites of a soil-surface type with different letters differ (P < 0.05).
[2] Means within microsites of a soil-surface type between trampling treatments with an asterisk differ (P < 0.05).

emergence of certain species appeared to be favored by certain kinds of microsites. The presence of some young plants in the sample suggests that some microsites also favor establishment.

Trampling Intensity Effects

Livestock trampling may alter depression and surface microsites. A shrub–Type I surface is not likely to be trampled because it is protected by the shrub canopy. Trampling a Type II surface could crush the pinnacles, fill the trenches, and effectively cover any seed present. Since soil of this surface type does not form a durable crust, restriction of seedling emergence should be minimal. Trampling a Type III surface could mix seed and soil and fill the cracks. Since soil of this surface type slakes when saturated and forms a durable crust when dry, seedling emergence could be severely restricted if drying occurs before seedlings emerge.

The influence of intensity of trampling by cattle on seedling density in various soil-surface microsites was studied on the Dinner Station 2 and McClelland Creek sites in northeastern Nevada (Table 1). Both sites are representatives of the basin big sagebrush, bluebunch wheatgrass [Agropyron spicatum (Pursh) Scribn. and Smith] habitat type. Estimated annual precipitation is

about 300 mm. Precipitation patterns probably resulted in at least average seedling emergence in the spring and survival of these seedlings until time of sampling. The Dinner Station 2 site has been moderately trampled for many years. Moderate trampling was defined as some cattle hoof prints over the entire site, few cattle trails with disturbed and pulverized soil surface, cryptogam cover evident, and soil-surface types and microsites readily visible after grazing. An untrampled site was provided by an exclosure that had excluded cattle for 1 year. The McClelland Creek site has been heavily trampled for many years. Heavy trampling was defined as the area completely covered by hoof marks, many cattle trails, most of the soil surface pulverized into dust, cryptogam cover missing, and soil-surface types and microsites difficult to recognize after grazing. The untrampled site was in an adjacent highway right-of-way that has been fenced for 11 years. Density of seedlings on pinnacle and in trench microsites of the Type II surface and on polygon or in crack microsites of the Type III surface was determined.

On the moderately trampled site, significantly more big sagebrush seedlings emerged on the untrampled (117/9 m^2) than on the trampled (96/9 m^2) area (Table 8). The opposite response occurred on the heavily trampled site, 4,814/9 m^2 in the untrampled area and 7,234/9 m^2 with trampling (Table 9). Both moderate and heavy trampling resulted in a greater density of big

Table 9. Mean density of big sagebrush, perennial bunchgrass, and perennial and annual forb seedlings in trench and on pinnacle microsites of the Type II surface and in crack and on polygon microsites of the Type III surface in June at the McClelland Creek site. The sites had been protected from trampling or heavily trampled for many years before sampling.

Species	Type II		Type III		Type II		Type III	
	Trench	Pinnacle	Crack	Polygon	Trench	Pinnacle	Crack	Polygon
	11-yr protection				Heavy trampling			
Shrub								
Big sagebrush	479*[2]	2521 a[1]*	341	1473 a*	339	3677 a	356	2862 a
Perennial grass								
Sandberg bluegrass	59 a*	6	18 a	4	25 a	6	11	8
Squirreltail	83 a*	9	13 a	3	33 a	17	15 a	7
Perennial forb								
Desert phlox	90 a*	6	106 a*	19	49 a	9	53 a	3
Wild onion	20*	19*	12	34 a*	4	2	7	9
Annual forb								
Cryptantha	35*	32*	17 a*	9	12	11	5	17 a
Gilia	177 a*	47	28	22*	72	63	28 a	2

(Between the header subtitles "11-yr protection" and "Heavy trampling" runs the unit label: No./9 m^2)

[1] Means within a trampling treatment between microsites of a soil-surface type with different letters differ ($P < 0.05$).

[2] Means within a microsite of a soil-surface type between trampling treatments with an asterisk differ ($P < 0.05$).

sagebrush seedlings on the polygon microsite than in the crack microsite of the Type III surface. This is an important result because the polygon microsite makes up a much larger proportion of the Type III surface than does the crack microsite. This result also agrees with that obtained in the natural population study. A possible explanation for this difference in seedling emergence between microsites is that the small seeds of sagebrush fall both on the surface of polygons and in cracks. Both moderate and heavy trampling may fill the cracks, perhaps to a depth that restricts the light required for germination of sagebrush seed (Weldon et al. 1959), or to a depth from which seedlings cannot emerge. Both moderate and heavy trampling may increase emergence on polygon surfaces by planting seed in mineral soil (McIlvanie 1942, Beetle 1960) so that conditions for germination are improved. Also, since March and April precipitation was well above normal in the sample year, reformed crust of the Type III polygon surface would be moist and soft following storm periods. Under these conditions seedling emergence is not restricted.

On the moderately trampled site, significantly more Sandberg bluegrass and squirreltail seedlings emerged in the trampled area than in the untrampled area (Table 8). Moderate trampling appeared to enhance seedling emergence, probably by planting seed lying uncovered in trenches and cracks and on the surface of pinnacles and polygons. On the heavily trampled site, fewer Sandberg bluegrass and squirreltail seedlings emerged in the trampled area compared to no trampling (Table 9). Heavy trampling apparently destroyed many microsites favorable to these species. On both the moderately and heavily trampled sites, generally more grass seedlings emerged from trenches and cracks than from pinnacles and polygons. Sandberg bluegrass was an exception possibly because the small seed of this species was planted too deep in depression microsites.

Moderate trampling of pinnacle and polygon microsites of Type II and III surfaces was not favorable or detrimental to emergence of seedlings of perennial forbs such as wild onion [Allium spp. L.], hawksbeard [Crepis acuminata Nutt.] and biscuitroot [Lomatium spp. Raf.]. Response of the annual forbs little flowered collinsia [Collinsia parviflora Lindl.] and microsteris on surface microsites was variable (Table 8). Moderate trampling of trench and crack microsites of Type II and III surfaces, however, generally reduced emergence of both perennial and annual forbs; desert phlox [Phlox austramontana Cov.] was the exception. In general, heavy trampling greatly reduced emergence of phlox and wild onion and of the annual forbs cryptantha [Crypantha spp. Lehm. ex G. Don] and gilia [Gilia spp. Ruiz and Pavon] on both surface and depression microsites of Type II and III surfaces (Table 9).

Table 10. Seedling emergence in early June and second-year survival in late July of the following year at sites in central and northern Nevada expressed as a percent of the number of live seeds planted.

Site	Treatments[3]	Artrw (78)		Sihy (90)		Posa (51)	
		June (%)	July (%)	June (%)	July (%)	June (%)	July (%)
Coils Creek	IT	9.0 a-c [1]	0.4 de	7.4 b-d	1.7 c-e	6.7 b-d	2.4 bc
	IIT	3.9 d	0.4 de	8.8 a-c	1.2 c-e	11.3 ab	4.4 a
	IIIT	2.6 d	0.0 e	9.0 a-c	0.0 e	13.0 a	4.0 ab
	IIICUT	3.2 d	0.0 e	2.9 d	0.0 e	9.1 a-c	2.8 a-c
	IIIPT	3.0 d	0.0 e	11.4 ab	1.3 c-e	11.1 ab	2.2 b-d
Paradise Valley	IT	23.8 c-e	1.4 b-e	35.1 a	3.9 ab	9.1 h-k	4.8 a
	IIT	7.5 i-l	1.4 b-e	28.6 a-d	0.9 c-e	17.0 e-h	3.6 a-c
	IIICT	2.4 k-l	0.9 c-e	24.8 b-e	0.0 e	18.6 e-g	2.9 a-d
	IIICUT	3.2 j-l	0.4 de	10.7 g-k	0.0 e	11.4 g-j	4.2 a
	IIIPT	7.7 i-l	0.5 de	13.1 f-i	0.0 e	14.0 f-i	4.4 a

[1] Emergence and survival means for Artrw, Sihy, and Posa followed by different letters differ (P < 0.05). Comparisons can be made among rows and columns for each date on each site.

[2] Artrw = Wyoming big sagebrush, Sihy = squirreltail, Posa = Sandberg bluegrass. Number in parenthesis following each species symbol is the number of live seeds planted based on germination tests.

[3] Numerals I, II, and III refer to soil-surface types. C and P refer to crack and polygon microsites, respectively. T and UT refer to trampled and untrampled surface, respectively.

Seeding and Simulated Trampling

In the previous two studies, the influence of microsite on percent emergence could not be determined because the density of viable seeds present was unknown. In this study, a known number of viable seeds was planted. Emergence and survival of seedlings of native and introduced grasses were determined from seed sown on different microsites and covered by simulated trampling, or left untrampled. This study was conducted in 3 years on five sites in central and northern Nevada (Table 1). Four sites represent the Wyoming big sagebrush/Thurber needlegrass habitat type. One site represents the basin big sagebrush/bluebunch wheatgrass habitat type. Seed of six species was sown: Wyoming big sagebrush, Sandberg bluegrass, Thurber needlegrass, squirreltail, 'Nordan' crested wheatgrass, and cheatgrass. Trampling was simulated by pounding the soil surface with a nail-studded mallet after seeding until the soil surface was powdered to a depth of 2 to 3 cm, similar to that after heavy cattle use. At two sites, location of each kind of microsite was charted prior to seeding and compared to the location of microsites in the following year.

Surface and depression microsites of the Type II and III surfaces tend to reform in the same position the year after simulated trampling. Therefore, the emergence and survival of individual plants can be related to a specific microsite.

In 1 year, less than 1% of the live seed planted by simulated trampling treatments on two sites in late summer produced seedlings the following spring. This poor seedling emergence was attributed to low winter-spring precipitation. In a second trial, seedling emergence in June, survival in July, and 2-year survival the following July were determined on five sites. Results from two locations, Coils Creek and Paradise Valley (Table 10), typify responses obtained for big sagebrush, squirreltail, and Sandberg bluegrass on other sites. Overall emergence was highest on sites where precipitation from October through June was estimated to be about 120 to 125% of average. Lower emergence occurred at sites where precipitation from October through June was estimated to be about 80 to 85% average. More sagebrush seedlings emerged on trampled Type I surface than on any other trampled surface. Emergence of squirreltail seedlings was variable but good emergence occurred with most treatment combinations, particularly at Paradise Valley (Table 10). Differences among treatment means for Sandberg bluegrass were not always significant, however, the general trend was for fewer seedlings on the trampled Type I surface. Small bluegrass seeds may have been planted too deep by simulated trampling on this friable surface. Data for crested wheatgrass, Thurber needlegrass, and cheatgrass are not shown in Table 10. However, emergence of the former two species on various soil surfaces and trampling treatments varied from 0.6 to 16.0%. A significant difference occurred only at one site where Thurber needlegrass emergence was 13.3% when seed was placed in cracks of the Type III

161

surface and covered by simulated trampling. Emergence of cheatgrass on the various trampled and untrampled surfaces varied from 3 to 33%. However, even on sites with low emergence, seedlings were found on most soil surfaces and trampling treatments. This response, particularly on the Type III surface, suggests a reason why cheatgrass is such a successful invader species.

Survival of seedlings into late July of the seedling year was greatest on trampled Type I surface under shrubs. Shade provided by shrub cover and a friable soil with litter cover probably created a more favorable microsite for survival than that present in the interspaces between shrubs.

Precipitation from October through July during the second year after seeding ranged from 75 to 95% of normal. Considerable seedling mortality occurred between sample dates (Table 10). Survival of sagebrush plants ranged from 0 to 1.4% (0 to 12, 2-year old plants/m^2) with no significant differences among soil-surface microsites or simulated-trampling treatments. Survival of squirreltail plants ranged from 0 to 3.9% (0 to 39 plants/m^2) with the most plants on the trampled Type I surface at Paradise Valley (Table 10). After 2 years, survival of bluegrass was significantly greater than that for sagebrush or squirreltail on most soil surfaces and microsites at most locations. All these plants cannot establish; many will die and others will coalesce to form the typical large clumps of bluegrass found under shrubs and in interspaces between shrubs.

In a third trial, trampled and untrampled treatments on Type I and II surfaces were compared. Both emergence and first-year survival were significantly higher, or tended to be higher, on the trampled Type I and II surfaces than on respective untrampled surfaces. An example of results showed that respective emergence on trampled vs. untrampled Type II surface was: 36.3 vs. 15.1% for sagebrush, 5.9 vs. 0.0% for Thurber needlegrass, 8.7 vs. 1.1% for squirreltail, 17.3 vs. 1.8% for crested wheatgrass, and 32.0 vs. 7.1% for cheatgrass. Respective survival on trampled and untrampled Type II surface was 1.5 vs. 0.9% for sagebrush, 2.9 vs. 0.0% for Thurber needlegrass, 3.7 vs. 0.1% for squirreltail, and 7.7 vs. 0.4% for crested wheatgrass. All differences were significant except for sagebrush survival.

THE INFLUENCE OF PRECIPITATION PROBABILITY ON SECONDARY SUCCESSION

Natural population and seeding studies (Stephens 1980, Eckert et al. 1986b) have shown that some plant establishment occurred in competitive situations on certain soil-surface types and microsites. Most established plants were of exotic or increaser species such as crested wheatgrass, cheatgrass, sagebrush, squirreltail, and Sandberg bluegrass. The question arises, what mechanism is responsible for the periodic

establishment of decreaser grasses? Noy-Meir (1973) and Went (1956) suggest that natural establishment of native species in harsh environments occurs only in years of unusually high precipitation. Episodic precipitation events of low probability and resulting increases in the amount and longevity of available soil water may be the principal mechanism by which the depressing effects of environmental stress are mitigated enough to allow secondary succession to advance. By identifying species response to periods of favorable soil water and to drought conditions, the land manager could use precipitation probabilities to more precisely state management objectives and to interpret reasons for recruitment or lack of recruitment of new plants of desirable species.

Methods

A 3-year study is underway to evaluate emergence and establishment of exotic and native increaser and decreaser grasses in response to precipitation probability treatments applied to Type II and III soil surfaces in cleared and brush areas. These two surfaces were selected because they are the most abundant in the shrub interspaces and because they are the surfaces on which secondary succession will most likely occur. Only preliminary results based on 1 year's data are presented.

The study is conducted on three range sites: Loamy 8-10", Loamy 10-12", and Claypan 10-12". All shrubs were removed from one set of plots in late July 1984. Seedings were made in early October 1984. In each of six replications in each brush treatment, four 0.1 m^2 plots were randomly located on Type II soil and four on Type III soil. Each of these plots was divided into four 250 cm^2 subplots and each subplot was seeded to either crested wheatgrass, bluebunch wheatgrass, squirreltail, or Thurber needlegrass. Seed was broadcast and mixed with the surface cm of soil. Seeding rate was 100 viable seeds per subplot. Four precipitation-probability treatments were randomized on the soil-surface plots: natural precipitation falling from May to the end of September 1985, 50% probability - simulated precipitation equal to 50% probability of a weekly amount of precipitation from May to the end of September, 25% probability and 5% probability (Gifford et al. 1967). The amounts of natural precipitation and simulated precipitation applied by these treatments are shown in Table 11. Simulated-precipitation treatments were applied in 1 day each week. A measured amount of water was applied from a sprinkler can over a plot frame that minimized movement of surface water among subplots and from the inside to the outside of the plot. Gypsum soil moisture blocks were placed at depths of 2.5, 5, 10, and 15 cm in two replications before seeding. Soil-water tensions were determined immediately before watering and at intervals of 1,2,3, and 4 days after watering. Seedlings were counted in May, June, August, and October 1985. In May 1986 a random sample of plots in the 5 and 25% simulated-

precipitation treatments was selected and the 5% treatment was continued during the spring, summer, and fall of the second growing season to evaluate the effect of additional water during this period on plant establishment.

Results

Spring 1985 - Emerged Seedlings

Simulated-precipitation treatments were not initiated until mid-May. Therefore, plant densities in early May (Table 12) represent the maximum natural seedling emergence from the fall 1984 planting. At this time, the effects of soil-surface properties had already been manifest. Subsequent data represent seedling growth and survival and plant establishment in response to soil-surface properties, brush competition, and simulated-precipitaton treatments. Crested wheatgrass and Thurber needlegrass had the highest initial seedling densities on both soil surfaces and brush treatments, however, this density accounts for only a small percentage of the viable seed planted. The very low emergence of bluebunch wheatgrass and squirreltail represent very poor regeneration capacities for these species. Emergence of bluebunch wheatgrass was generally highest on the Loamy 10-12" site, the site where this species is an important component of the Potential Natural Community. Emergence of both crested wheatgrass and Thurber needlegrass was significantly greater on Type II surface than on Type III soil at all locations and on both brush treatments. Densities of bluebunch wheatgrass and squirreltail did not vary with type of soil surface on any site. Seedling size of all species was similar in both brush treatments.

Plant density in October represents seedlings surviving the first growing season (Table 13). Even the highest density of surviving plants account for only a very small percentage of the number of viable seeds planted. This low reproduction is further exacerbated under natural conditions by the very low seed rain shown for recent years (Table 14), even in the wet years of 1983 and 1984. Responses to variables were similar to those on the other three sample dates, i.e., crested wheatgrass generally had the highest overall density with Thurber needlegrass generally second ranked; density of these two species was greater on Type II surface than on Type III surface; density of crested wheatgrass generally was higher than for other species on either surface; and very low density of Thurber needlegrass, bluebunch wheatgrass, and squirreltail on the Type III surface of the Loamy 8-10" and Claypan 10-12" sites. Plant densities of crested wheatgrass and Thurber needlegrass were similar in both brush treatments. However, plants of these species were twice as tall and more plants had multiple culms on the cleared area than on the control.

The precipitation probability main effect; and the soil x precipitation, species x precipitation, and soil x species x precipitation interactions were significant only on the cleared area of the Claypan 10-12" site (Table 15). Crested wheatgrass density on Type II surface was generally similar on natural and the 5 and 25% treatments; on Type III surface only the 5% treatment increased density over natural precipitation. For Thurber needlegrass on Type II surface, densities on the 5, 25, and 50% treatments were greater than with natural precipitation. No precipitation treatment affected an increase in the density of Thurber needlegrass on Type III surface.

Soil-Water Regime for the Seedling Year

Soil water on all sites was depleted below -1.5 MPa to a depth of 46 cm by June 21. Therefore, the majority of water available to seedlings after this date was that provided by the simulated-precipitation treatments. Only the 5 and 25% treatments supplied soil water for seedling growth and survival after the middle of June. Interpretations based on data for the 25% probability treatment indicate that: 1) soil water was not available at 5 cm from the middle of June to the end of September, 2) from mid-June to the end of September, soil water at 2.5 cm was available for seedling growth and survival for only 1 day per week. Interpretations based on data for the 5% probability treatment indicate that: 1) soil water was not available below 5 cm from the middle of June until the end of September, 2) from mid June to the end of September, soil water at 2.5 cm was available for seedling growth and survival for 1 and sometimes 2 days per week, and 3) soil water at 5 cm was available for seedling growth and survival for 2 and sometimes 3 days per week.

Density and Height of Surviving Plants

Spring 1986. Plants present in spring 1986 from fall 1984 seeding (Table 16) represent 1-year old individuals that survived one growing season and one winter. Plant density followed the same trend as that in October 1985 on both brush and cleared areas, i.e., crested wheatgrass had the greatest number of plants in most comparisons, was equal to Thurber needlegrass in some comparisons, Thurber needlegrass generally was second ranked, and generally more plants of crested wheatgrass and Thurber needlegrass occurred on Type II surface than on Type III surface. Both the 5 and 25% precipitation treatments on Type II surface were generally most favorable for crested wheatgrass and Thurber needlegrass. In October 1985, simulated-precipitation treatments were significant in only two of six comparisons. In spring 1986, however, precipitation treatments were significant in five of six comparisons. This response suggests that additional soil water during the previous growing season was important to future survival of plants on the harsher sites and treatments. Although density of surviving plants in spring 1986 was similar on brush and cleared areas, plants in the brush area on all sites resembled large seedlings with a single culm. On cleared areas, plants had

Table 11. Total of natural and simulated precipitation on each treatment for spring 1985-emerged seedlings.

Ecological site and precipitation treatment	1984-85 (cm)	May[1] (cm)	June (cm)	July (cm)	Aug (cm)	Sept[2] (cm)	Total (cm)
Loamy 8-10"							
Natural, Oct-May	11.2						
Natural, by month		2.5	1.3	1.3	0.2	1.3	6.6
50% probability		5.5	2.8	2.6	0.7	2.6	14.2
25% probability		6.3	4.1	3.1	1.0	3.1	17.6
5% probability		9.4	8.9	7.4	4.3	5.4	35.4
Loamy 10-12"							
Natural, Oct-May	14.2						
Natural, by month		2.0	1.3	1.5	0.5	1.5	6.8
50% probability		4.8	2.8	3.0	1.3	3.0	14.9
25% probability		6.3	4.3	3.5	1.8	3.8	19.7
5% probability		11.4	11.2	9.6	5.8	7.1	45.1
Claypan 10-12"							
Natural, Oct-May	9.4						
Natural, by month		2.5	0.8	1.0	0.2	1.3	5.8
50% probability		5.5	1.8	2.0	0.7	2.6	12.6
25% probability		6.6	3.3	2.8	1.2	3.1	17.0
5% probability		9.9	9.7	7.8	4.8	6.1	38.3

[1] From May 7
[2] Until Sept 23

Table 12. Mean seedling density of four species on two soil-surface types on three ecological sites with shrub cover for the first sample date in 1985 (May). Plots were planted with 100 viable seeds in Oct. 1984.

	Loamy 8-10"		Loamy 10-12"		Claypan 10-12"	
Species	Type II	Type III	Type II	Type III	Type II	Type III
			No./250 cm^2			
Crested wheatgrass	9.1 a[1]	6.6 b	8.9 a	5.7 b	6.0 a	2.7 b
Bluebunch wheatgrass	1.0 c	0.1 c	3.2 c	2.9 c	1.4 bc	0.5 c
Squirreltail	0.2 c	0.2 c	0.4 d	0.4 d	1.4 bc	0.2 c
Thurber needlegrass	5.0 b	0.1 c	10.4 a	5.3 b	4.7 a	0.5 c

[1] Means within columns and rows for each ecological site with different letters differ (P < 0.05).

Table 13. Mean seedling density of four species on two soil-surface types on three ecological sites with shrub cover for the last sample date in 1985 (Oct.). Plots were planted with 100 viable seeds in Oct. 1984.

	Loamy 8-10"		Loamy 10-12"		Claypan 10-12"	
Species	Type II	Type III	Type II	Type III	Type II	Type III
			No./250 cm^2			
Crested wheatgrass	6.7 a[1]	2.9 b	5.5 b	1.6 c	4.3 a	1.5 b
Bluebunch wheatgrass	0.8 c	0.0 c	2.0 c	2.0 c	1.4 bc	0.4 cd
Squirreltail	0.2 c	0.0 c	0.0 c	0.0 d	0.1 d	0.0 d
Thurber needlegrass	3.5 b	0.2 c	7.3 a	2.8 c	2.4 b	0.2 d

[1] Means in columns and rows for each ecological site with different letters differ (P < 0.05).

Table 14. Mean density of viable seeds of crested wheatgrass and of native species in three years. Seed density was calculated from seed yields, weight/100 seeds, and percent germination data.

Species	1984	1984	1984
	----- No./250 cm^2 -----		
Crested wheatgrass	25	6	12
Bluebunch wheatgrass	2	2	1
Squirreltail	10	2	2
Thurber needlegrass	<1	<1	<1
Sandberg bluegrass	170	40	6

Table 15. Mean seedling density of two species in Oct. 1985 on the cleared areas of the Claypan 10-12" ecological site in response to soil-surface type and precipitation-probability treatments.

	Crested wheatgrass		Thurber needlegrass	
Precipitation probability	Type II	Type III	Type II	Type III
	--------- No./250 cm^2 -----------			
Natural	5.0 b[1]	1.7 d	2.2 c	0.3 c
50%	3.2 c	2.3 cd	5.3 b	0.7 c
25%	7.5 a	2.7 cd	8.2 a	0.5 c
5%	6.2 ab	4.5 bc	4.8 b	1.0 c

[1]Means in columns and rows for species followed by different letters differ (P < 0.05).

Table 16. Mean density in May 1986 of 1-year old plants of four species on the brush area of two ecological sites in response to precipitation-probability treatments. Plots were planted in Oct. 1984 with 100 viable seeds. Seedlings emerged in spring 1985.

	Loamy 8-10"				Claypan 10-12"			
				Precipitation probability				
Species	Natural	50	25	5	Natural	50	25	5
	--------------------------------- No./250 cm^2 -----------------------------------							
Crested wheatgrass	1.2 cd[1]	0.8 d	3.9 b	6.0 a	0.1 b	0.1 b	1.8 a	1.3 a
Bluebunch wheatgrass	0.2 d	0.1 d	0.2 d	0.8 d	0.0 b	0.0 b	0.0 b	0.0 b
Squirreltail	0.1 d	0.0 d	0.0 d	0.1 d	0.0 b	0.0 b	0.0 b	0.0 b
Thurber needlegrass	1.5 cd	0.5 d	0.4 d	2.2 c	0.0 b	0.2 b	1.8 a	1.2 a

[1]Means in columns and rows for each ecological site followed by different letters differ (P < 0.05).

Table 17. Mean density of plants of four species in Oct. 1986 after two growing seasons on the brush area of three ecological sites. Plots were planted in Oct. 1984 with 100 viable seeds. Seedlings emerged in spring 1985.

	Ecological site		
Species	Loamy 8-10"	Loamy 10-12"	Claypan 10-12"
	------------------------- No./250 cm^2 -------------------------		
Crested wheatgrass	3.5 a[1]	1.3 b	1.8 a
Bluebunch wheatgrass	0.3 bc	0.3 c	0.5 b
Squirreltail	0.0 c	0.3 c	0.0 b
Thurber needlegrass	0.9 b	2.4 a	1.5 a

[1]Means for each ecological site followed by different letters differ (P < 0.05).

multiple culms that formed small bunches with a basal diameter of up to 3 cm.

Fall 1986. Plants present in fall 1986 (Table 17) represent survival at the end of the second growing season. These data are means of the unwatered and watered treatments that were continued during the second growing season because these treatments were not significantly different in any comparison. Plant density was higher on Type II surface than on Type III surface on both the brush and clear areas of the Loamy 8-10" and Claypan 10-12" sites. Plant densities on the two soil-surface types were similar on the Loamy 10-12" site where Type II and Type III surfaces are more similar. These trends were evident throughout the study. Respective plant densities on the Loamy 8-10" site for Type II and III surfaces were 1.8 and

0.5/250 cm^2; for the Claypan 10-12" site, 1.6 and 0.3/250 cm^2. Crested wheatgrass had the highest survival on the Loamy 8-10" site, Thurber needlegrass density was highest on the Loamy 10-12" site, and both species had similar densities on the Claypan 10-12" site (Table 17).

Plants surviving until October 1986 on all sites, most brush treatments, both soil-surface types, and all simulated-precipitation treatments were similar in size. Although a few plants on both brush treatments on the Loamy 8-10" and Loamy 10-12" sites resembled large, single-culmed seedlings, most crested wheatgrass plants were up to 18 cm tall; bluebunch wheatgrass up to 13 cm, and Thurber needlegrass up to 11 cm. These plants had multiple culms and were in distinct bunches. On the brush area of the Claypan 10-12" site, plants of all species did not exceed 6 cm. On the cleared area, however, plants were similar in size to those on the other sites. The cleared areas of the Loamy 8-10" and Claypan 10-12" sites were the only situation in which crested wheatgrass alone produced reproductive culms up to 36 cm high.

SUMMARY AND CONCLUSIONS

Land management agencies presently are monitoring trends in range condition and interpreting these trends based on management objectives. Knowledge of the rate of, and reasons for, secondary succession are required for the factual statement of objectives and the accurate interpretation of vegetation change. This paper summarizes the influence of soil-surface type and precipitation probability on seedling emergence and survival, and on plant establishment.

Soil profiles were described on 23 sites in central and northern Nevada and soil surfaces were defined. Four distinctive soil-surface types occur on Xerollic argids and orthids of loess-influenced soils in the Intermountain area. These surfaces differ in morphological, chemical, and physical properties. They also differ in vegetative cover, genesis, and reformation characteristics. Due to these differences, these surfaces are either favorable or unfavorable for seedling emergence and, therefore, can affect natural revegetation and result in either secondary succession or retrogression.

A larger proportion of a favorable surface is associated with rangelands in high ecological condition. More of the unfavorable surfaces is associated with rangelands in low ecological condition. Natural plant populations show that different soil surfaces and associated depression and surface microsites can influence emergence of desirable and undesirable species. Moderate trampling appears to favor emergence of perennial grasses on all microsites, is not detrimental to emergence of perennial forbs on surface microsites, but is detrimental to emergence of perennial forbs in depression microsites. Heavy trampling is detrimental to the emergence of perennial grasses and forbs on all microsites, but favors emergence of sagebrush on surface microsites.

Precipitation probability was evaluated as a mechanism by which the depressing effects of environmental stress are mitigated enough to allow secondary succession to occur. Simulated precipitation and its interactions with soil-surface types and species influenced first-year survival of seedlings on one of three ecological sites studied. On this site, the 5 and 25% precipitation probability treatments resulted in greater seedling densities than did the 50%- and natural-precipitation treatments. Such a response occurred on only one site in spite of the fact that both the 5 and 25% treatments decreased soil-water tensions at 2.5 and 5 cm for 1 to 3 days on all sites. Precipitation treatments influenced the density of 1-year-old plants, suggesting that additional soil water in the previous growing season was important to survival of plants over winter. Additional water during the second growing season did not influence establishment of 2-year-old plants.

Throughout the study the general trend was for more plants of crested wheatgrass than for the other three species; Thurber needlegrass was generally second ranked, and more plants of these two species occurred on Type II surface than on Type III surface.

LITERATURE CITED

Anderson, D.C., K.T. Harper, and R.C. Holmgren. 1982. Factors influencing development of cryptogamic crusts in Utah deserts. J. Range Manage. 35:180-185.

Beetle, A.A. 1960. A study of sagebrush, the section of Tridentatae of Artemisia. Wyoming Agr. Exp. Stn. Bull. 368. 83 p.

Blackburn, W.H. 1975. Factors influencing infiltration rate and sediment production of semiarid rangeland soils in Nevada. Water Resources Research 11:929-937.

Eckert, R.E., Jr., F.F. Peterson, and J.T. Belton. 1986a. Relation between ecological range condition and proportion of soil-surface types. J. Range Manage. 39:409-414.

Eckert, R.E., Jr., F.F. Peterson, M.K. Wood, and W.H. Blackburn. 1977. Properties, occurrence and management of soils with vesicular surface horizons. Final Rep. Contract 5250-CT5-(N) between the USDI, Bureau of Land Management and the Nevada Agr. Exp. Stn. 116 p.

Eckert, R.E., Jr., F.F. Peterson, M.S. Meurisse, and J.L. Stephens. 1986b. Effects of soil surface morphology on emergence and survival of seedlings in big sagebush communities. J. Range Manage. 39:414-421.

Eckert, R.E., Jr., M.K. Wood, W.H. Blackburn, F.F. Peterson, J.L. Stephens, and M.S. Meurisse. 1978. Effects of surface-soil morphology on improvement and management of some arid and semiarid rangelands. In D.N. Hyder, (ed.) Proc. First Internat. Rangeland Cong. Denver, CO. p. 299-302.

Evaneri, M., D.H. Yaslon, and Y. Gutterman. 1974. Notes on soils with vesicular structure in deserts. Z. Geomorph. N.F. (18:92) 162-172.

Evans, R.A., H.R. Holbo, R.E. Eckert, Jr., and J.A. Young. 1970. Functional environment of downy brome communities in relation to weed control and revegetation. Weed Sci. 18:154-162.

Evans, R.A., and J.A. Young. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. Weed Sci. 18:697-702.

Evans, R.A., and J.A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. Weed Sci. 20:350-356.

Gifford, R.O. G.L. Ashcroft, and M.D. Magnuson. 1967. Probability of selected precipitation amounts in the western region of the United States. Section for Nevada. Nevada Agr. Exp. Stn. T 8. Unnumb.

Gifford, R.O., and D.F. Thran. 1969. Equipment for the measurement of emergence force of seedlings. Crop Sci. Abstr. p. 23. West. Soc. Crop Sci., Reno, NV.

Guthrie, R.L., and J.E. Witte. 1982. New designations for soil horizons and layers and the new Soil Survey Manual. Soil Sci. Soc. Amer. J. 46:443-444.

Harper, J.L., J.T. Williams, and G.R. Sanger. 1965. The behavior of seed in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants. J. Ecol. 53:273-286.

Hillel, D. 1959. Studies on loessial crusts. Agr. Res. Sta., Rehovath-Beit, Daga, Israel, Bull. 63.

Hillel, D. 1960. Crust formation in loesseal soils. Trans. 7th Int. Cong. Soil Sci. 1:330-339.

Hugie, V., and H.B. Passey. 1964. Soil surface patterns of some semiarid soils in northern Utah, southern Idaho and northeastern Nevada. Soil Sci. Soc. Amer. Proc. 28:786-792.

Lapham, M.H. 1932. Genesis and morphology of desert soils. Amer. Soil Surv. Assoc. Bull. 13:34-52.

Loope, W.L., and G.F. Gifford. 1972. Influence of microfloral crust on selected properties of soils under pinyon-juniper in southeastern Utah. J. Soil and Water Conserv. 27:164-167.

McIlvanie, S.K. 1942. Grass seedling establishment and productivity - overgrazed and protected range soils. Ecol. 23:228-231.

Melton, F.A. 1940. A tentative classification of sand dunes, its application to dune history in the southern high plains. J. Geol. 48:113-174.

Miller, D.E. 1971. Formation of vesicular structure in soils. Soil Sci. Soc. Amer. J. 35:635-637.

Miller, D.E. 1973. Water retention and flow in layered soil profiles. In: R.R. Bruce, K.W. Flach, and H.M. Taylor (eds.) Field Soil Water Regime. Soil Sci. Soc. Amer. Special Publ. No. 5. p. 107-118.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Eco. Sys. 4:25-51.

Pendleton, D.F., J.W. Menke, W.A. Williams, and R.G. Woodmansee. 1983. Annual grassland ecosystem model. Hilgardia 51:44 p.

Range Inventory Standardization Committee. 1983. Guidelines and terminology for inventories and monitoring. Soc. for Range Manage., Denver, CO. 13 p.

Schlatterer, E.F. 1968. Establishment and survival of three native grasses under natural and artificial conditions. M.S. Thesis, Univ. of Idaho. 94 p.

Springer, M.E. 1958. Desert pavement and vesicular layer of some soils of the desert of Lahontan Basin, Nevada. Soil Sci. Soc. Amer. Proc. 22:63-66.

Stephens, J.L. 1980. Seedling emergence on vesicular crusted surfaces as affected by artificial and natural cattle trampling. M.S. Thesis, Univ. of Nevada-Reno. 116 p.

Stuart, D.M., G.E. Schuman, and A.S. Dylla. 1971. Chemical characteristics of the coppice dune soils in Paradise Valley, Nevada. Soil Sci. Soc. Amer. Proc. 35:607-611.

Stuart, D.M., R.E. Eckert, Jr., A.S. Dylla, and G.E. Schuman. 1973. Seeding coppice dune areas in northern Nevada. Nevada Agr. Exp. Stn. T 11. 17 p.

Taylor, H.M. 1971. Seedling emergence of wheat, grain sorghum, and guar as affected by rigidity and thickness of surface crusts. Soil Sci. Soc. Amer. Proc. 26:431-433.

Tueller, P.T. and W.H. Blackburn. 1974.
    Condition and trend on the big
    sagebrush/needle and thread habitat type in
    Nevada. J. Range Manage. 27:36-40.

USDA. 1951. Soil Survey Manual. USDA Agr. Res.
    Adm. Handbk. No. 18. 503 p.

USDA. 1975. Soil taxonomy. USDA, Soil
    Conservation Service. Agr. Handbk. No. 436.
    754 p.

USDA. 1976. National Range Handbook. NRH-1
    Soil Conservation Service, Washington, D.C.
    Unnumb.

Weldon, L.W., W.D. Bohmont, and H.P. Alley.
    1959. The interrelations of three
    environmental factors affecting germination
    of sagebrush seed. J. Range Manage.
    12:236-238.

Went, R.W. 1956. The ecology of desert
    plants. Sci. Amer. 192:68-75.

Wight, J.R. (ed.) 1983. SPUR - Simulation of
    Production and Utilization on Rangelands.
    U.S. Dept. Agr., Misc. Pub. No. 1431. 120 p.

Wood, M.K. 1976. The effects of vesicular
    horizons on emergence of grasses and
    shrubs. M.S. Thesis, Univ. of Nevada,
    Reno. 74 p.

Wood, M.K., W.H. Blackburn, R.E. Eckert, Jr. and
    F.F. Peterson. 1978. Interrelations of the
    physical properties of coppice dune and
    vesicular dune interspace soil with grass
    seedling emergence. J. Range Manage.
    31:189-192.

Wood, M.K., R.E. Eckert, Jr., W.H. Blackburn, and
    F.F. Peterson. 1982. Influence of crusting
    soil surfaces on emerged and establishment of
    crested wheatgrass, squirreltail, Thurber
    needlegrass, and fourwing saltbush. J. Range
    Manage. 35:282-287.

Young, J.A., and R.A. Evans. 1986. Erosion and
    deposition of fine sediments from playas.
    J. Arid Environ. 10:103-115.

Young, J.A., R.A. Evans, and R.E. Eckert, Jr.
    1969. Population dynamics of downy brome.
    Weed Sci. 17:20-26.

SEEDBED PREPARATION AND SEEDING TECHNIQUES IN SOUTHERN AFRICA

Norman F. G. Rethman[1]

ABSTRACT

As a result of the wide diversity of environments on the subcontinent, a wide range of both tropical and temperate species are adapted for use in planted pastures and in range reinforcement programs. This paper reviews recommendations and experience with respect to four tropical pasture species (Anthephora, Cenchrus, Eragrostis and Digitaria), and range reinforcement work in grassland areas receiving relatively high rainfall (>600 mm per annum). Successful establishment of these species is dependent on fine tilth, moisture conservation, weed control and compaction to ensure good soil seed contact of the shallow placed seed. Seeding rates and times are adjusted to different agro-ecological areas. In range reinforcement work in the high rainfall conditions a range of grasses have been successfully established with no, or minimal, soil disturbance and overseedig provided competition was reduced and fertility status was corrected. Sod seeding, with an implement combining cultivation, liming, fertilization, seeding and compaction was, however, necessary to successfully establish legumes in range.

INTRODUCTION

Southern Africa is characterized by a wide range of rainfall conditions. Only 8% of the sub-continent receives more than 750 mm per annum, 25% receives 500-750 mm, 37% receives 250-500 mm and 30% receives less than 250 mm. Seasonal distribution varies from summer to winter. Coupled with altitudes varying from sea level to 3000 m and a varied geology, this results in a wide diversity of agro-ecological conditions and species being used for planted pasture and range reinforcement.

In this paper, with the objective of reviewing seedbed preparation and seeding techniques on the sub-continent, it was decided to concentrate on some of the most important pasture species established under dryland conditions in the summer rainfall areas. Also included is a brief review of range reinforcement in grassland areas receiving more than 600 mm per annum.

[1]Professor Grassland Science, Department of Plant Production, University of Pretoria, Pretoria 0002, Republic of South Africa.

The species to be discussed are Anthephora pubescens Nees (bristlegrass), Cenchrus ciliaris L. (blue buffelgrass), Eragrostis curvula (Schrad.) Nees. (weeping lovegrass), and Digitaria eriantha Steud. subsp. eriantha (Smuts fingergrass).

REVIEW

Anthephora pubescens

This grass is well adapted to semi-arid areas receiving less than 500 mm per annum. It does not do well where yearly rainfall exceeds 600 mm and tends to decrease during periods of above average rainfall. Under these conditions availability of, and competition for, moisture is of paramount importance. Seedbed preparation thus emphasizes improved permeability, conservation of sub-soil moisture reserves and efficient weed control.

Establishment is usually during the late summer (February-March) when high maximum temperatures, characteristic of these agro-ecological areas, are less of a limiting factor. At this time soil moisture conditions are better than in spring or early summer. Although a wide variety of implements have been used to establish bristlegrass, the most effective technique has been the placement of seed in the wheel tracks of a tractor and compacting the seed into the soil with the rear wheels.

Espacement and seeding rate are linked with moisture conditions. In the drier range of its adaptation (300-400 mm) bristlegrass is planted in 750-900 mm rows. With better moisture conditions 450 mm rows are recommended, and broadcasting is used where the average annual rainfall exceeds 500 mm. The seeding rates used vary from 5 kg ha^{-1}, with the wider espacement to 8 kg ha^{-1} with narrow row espacements or broadcast stands.

In areas receiving 450-600 mm of rain, alternate rows of bristlegrass and alfafa (Medicago sativa) using seeding rates of 3 kg and 5 kg ha^{-1} respectively are being recommended to improve the quality of forage and to reduce dependence on nitrogenous fertilizer. A relatively recent development in Southern Africa has been the use of seed coating, which, when used on "fluffy" grass seeds, simplifies seeding and effectively reduces seeding rates (Dickenson, et al., 1984; Kruger, et al., 1985).

Cenchrus ciliaris

Blue buffelgrass is adapted to a wider range of moisture conditions than is bristle grass.

It produces well under rainfed conditions of 400 mm per annum and above and has the potential of very high yields (30 tDM ha^{-1}) under irrigation. The main limitations of the species are a preference for heavier soils and a sensitivity to winterkill in colder areas. Both factors have a direct bearing on successful establishment.

As with all dryland establishments, but especially in the drier areas, emphasis in seedbed preparation is placed on a fine but permeable soil tilth ensuring good infiltration and storage of moisture reserves. Weed control to eliminate competition for this moisture is also of cardinal importance.

As with bristle grass, establishment is usually in late summer (February-March). In those areas experiencing severe winters, however, an earlier planting time (December-January) is preferred to ensure a certain degree of maturity before the onset of winter.

Espacement and seeding rate are linked with the moisture status of each site. Recommendations do, however, vary widely. Whereas Dickinson et al. (1984) recommend 1-1.5 kg ha^{-1} in 1000-1500 mm rows for drier conditions and 4-5 kg ha^{-1} for broadcast stands under irrigation, Kruger et al. (1985) recommend 5 kg ha^{-1} for irrigated broadcast stands. The recommendations of Cross (1978) are similar to those of Dickinson et al. (1984) with 2-3 kg ha^{-1} being recommended for row plantings and 4-6 kg ha^{-1} for broadcast stands. All workers place particular emphasis on the use of certified seed with good germination. This can only be achieved by allowing for an after-ripening period of 9-12 months and avoiding the use of freshly harvested seed.

Whatever implement is used to plant blue buffelgrass, the application of the following guidelines will improve the probability of successful establishment:

: sow seed on a dry topsoil with a good moisture reserve in the subsoil;

: compact after sowing;

: apply corrective fertilization (blue-grass is particularly sensitive to P-deficiencies);

: allow to grow out before use.

As with bristlegrass, the use of seed coating is simplifying the planting of fluffy Cenchrus seed. Other developments have been the establishment of mixtures with alfafa, usually based on alternate rows at seeding rates of 2-5 kg buffelgrass and 3-10 kg alfafa ha^{-1}, depending on the moisture status, and the use of widely spaced corn

(Zea mays) as a nurse crop. With respect to the latter alternative, corn is planted in 1500-2100 mm rows and the blue buffelgrass is interplanted when the moisture requirements of the corn are decreasing.

Eragrostis curvula

Weeping lovegrass ecotypes used for planted pastures in Southern Africa have been adapted to the high rainfall (600 mm per annum) regions and research has been concentrated in these regions, where virtually all plantings are established and utilized under dryland conditions. Accepting that the principles of a fine but permeable seed bed, efficient moisture conservation and weed control are as applicable to this pasture as to other dryland pastures, attention will be focussed on seeding rate, depth of seeding, time of establishment and mixtures in the following discussion.

Seeding Rate

With the exception of dry situations linked with rainfall of less than 500 mm and/or soil texture, drainage and depth, virtually all weeping lovegrass is established in broadcast stands. Row plantings on "dry" sites are usually in 450-900 mm rows at rates varying from 0.5-1.5 kg ha^{-1} (Rethman, 1973), 2 kg ha^{-1} (Rethman, 1974; Kruger et al., 1985), 2-3 kg ha^{-1} (Cross, 1978) to 3 kg ha^{-1} (Fair, 1986). The lower recommendations appear to have been made when there was a shortage of seed, or by workers from a drier environment. Broadcast plantings on sites with a better moisture status also vary tremendously. Whereas Rethamn (1973) reported that 1-2 kg ha^{-1} would give a satisfactory stand under good conditions, the majority of workers play it safe with recommendations of 4 kg ha^{-1} (Rethman, 1974; Kruger et al., 1985), 4-6 kg ha^{-1} (Rethman, 1973; Cross, 1978), 5 kg ha^{-1} (Dickinson et al., 1984) and 6-8 kg ha^{-1} (Fair, 1986) being the order of the day.

Seeding Depth

In this respect, all workers emphasize shallow placement with rolling before and after seeding to effectively place the seed at a depth of 6-12 mm in close contact with the soil.

Seeding Time

Weeping lovegrass has been successfully established in spring, summer and autumn, but the summer months are generally avoided in the warmer areas. In the eastern highlands at an altitude of 1600-2000 m above sea level summer temperatures are not as critical, with the distribution and dependability of rainfall and the frost-free period being more important in determining the time of establishment. In general, where moisture is

not limiting, where winters are mild and where weed problems mitigate against early season plantings, autumn plantings are to be preferred provided that germination takes place at least four weeks before frost. Other areas have more dependable rainfall in the early season and producers aim to maximize yields in the year of establishment by planting in spring (Rethman, 1973; Fair, 1986).

Seeding Mixtures

There are two basic reasons for planting weeping lovegrass in a mixture. Firstly, it is often planted with a nurse crop of Eragrostis teff (Teff), a fine stemmed annual hay crop, with the objectives of increasing yields in the establishment season and suppressing a broadleafed weed problem. The proportions of lovegrass and teff on the basis of kg ha^{-1} recommended by different workers vary from 2:5 (Rethman, 1973), 4:6 (Rethman, 1974), 2:6 (Kruger et al., 1985), 5:5 (Dickinson et al., 1984) to 6:3 (Fair, 1986).

Secondly, increasing use of lovegrass/legume mixtures, with the objective of reducing input costs and improving quality, are being made. In areas receiving less than 850 mm per annum, alfafa is the preferred legume, but the proportions vary with Dickinson et al. (1984) recommending 1.5-2 kg lovegrass and 5-7 kg alfafa ha^{-1}, Kruger et al. (1985) suggesting 2 kg lovegrass and 10 kg alfafa ha^{-1} and Fair (1986) recommending a ratio of 3:4 kg ha^{-1} for alternate row plantings and 6:10 kg ha^{-1} for a broadcast mixture. Rethman and de Witt (1984), in reporting on a comparison of different mixed stands with pure stands of lovegrass and alfafa, found that the best results were obtained from a seeding mixture of 1.5:15 kg ha^{-1} compared with mixtures of 2:10 kg ha^{-1}. Better results have generally been obtained from alternate row plantings than from broadcast mixtures with respect to eveness of stand and utilization by grazing animals.

In high rainfall areas (more than 850 mm per annum) Dickinson et al. (1984) recommends that red and white clover (Trifolium pratense) and T. repens respectively) be seeded with lovegrass in the ratio of 2:1:1 kg ha^{-1} (grass, red clover, white clover). Although the clovers are better adapted to these environmental conditions than alfafa, it remains a problem to maintain a balance between lovegrass and clover because of the different management requirements. As opposed to this, Rethman and de Witt (1984) found lovegrass and alfafa to be very compatible with respect to management requirements and utilization by grazing animals.

Digitaria eriantha

Smuts fingergrass is notorious for poor establishment and this is probably the reason for its relatively recent acceptance. Although showing promise prior to World War II, a poor germination and establishment record until the mid-70s mitigated against its widespread utilization. Because of this, advisers place particular emphasis on condition of the seedbed, moisture conservation, weed control and corrective fertilization before considering seeding rate, depth, time and mixtures.

Seeding Rate

As with the foregoing species, recommendations vary widely. Probably the biggest reason for this variation is the variable germination rate caused by the necessity for a post harvest ripening period of 9-12 months to ensure good germination. With this variation between batches of seed, it is not surprising that rates varying from 2-12 kg ha^{-1} for broadcast stands have been made (Cross, 1978; Dickinson et al., 1984; Kruger et al., 1975; Rethman, 1985; Fair, 1986). Recommendations for row establishment have varied from 1 kg ha^{-1} (Dickinson et al., 1984) to 5-6 kg ha^{-1} (Cross, 1978; Fair, 1986). Intermediate rates of 2, 3 and 4 kg ha^{-1} have been suggested by Kruger et al. (1985), Fair (1986) and Rethman (1985) respectively. Rethman (1985) has, in fact, reported that when using good quality seed no improvement was obtained when seeding rates were increased from 2 to 8 kg ha^{-1}.

Seeding Depth

This grass should preferably be sown on the surface and firmed into the soil with a press wheel or tractor tire to achieve a seeding depth of 5-10 mm (Dickinson et al., 1984); Fair, 1986).

Seeding Time

It is the general consensus that the best time to plant Smuts fingergrass is during the summer months when moisture is least likely to be limiting. Dickinson et al., (1984) suggest November/February, whilst Kruger et al. (1985) have suggested January/March. All workers concur that seedlings should be well established before the onset of killing frosts.

Seeding Mixtures

Smuts fingergrass has been established with varying degrees of success with nurse crops such as teff or Rhodes grass (Chloris gayana). Whilst the former is an annual, the latter often persists for 2-3 seasons. The seeding mixture for fingergrass and teff recommended by Rethman (1985) is 4:6 kg ha^{-1} respectively. Fingergrass/Rhodes

grass mixtures vary from 5:3 to 4:4
kg ha^{-1} (Dickinson et al., 1984; Rethman,
1985). Combining the grass with Panicum
maximum, arrowleaf clover (Trifolium
vesiculosum) and alfafa at rates of 4:4, 2:5
and 2:6 kg ha^{-1} respectively has also
yielded promising results, indicating the
versatility of this species (Dickinson et
al., 1984; Rethman, 1985).

Range Reinforcement

Improving or reclaiming rangeland by the
introduction of improved pasture species has
met with minimal success in the drier parts
of Southern Africa. Some success has been
achieved in the higher rainfall areas and it
is worthy to note that specific problems had
to be overcome before this was achieved.

Edwards (1978) concluded that in order to
succeed with a range reinforcement program
the following aspects should receive
attention. Firstly, competition from
existing vegetation should be reduced,
minimized or eliminated by the use of
herbicides, cultivation, trampling and/or
fertilization. In this respect,
fertilization and tine-cultivation has been
used with success[1] on the Western Transvaal
Highveld (600 mm per annum) to establish
Smuts fingergrass in degraded range. Rethman
and Beukes (1973) also used fertilization to
establish weeping lovegrass in dense
grassland of the Eastern Transvaal Highveld
(750 mm per annum), and the Fertilizer
Society of South Africa[2] also had success
with overseeding temperate species such as
Festuca and Dactylis into dense fertilized
grassland of the Drakensberg foothills
(900-1000 mm per annum). On lithosolic soils
of the Eastern Transvaal escarpment,
Pennisetum clandestinum (kikuyu)[3] was
totally dominant within 12 months of seeding
provided that the existing grass was
eliminated (by herbicides or trampling), that
seed was placed in an organic mulch or dung
pat (germination of seed fed to ruminants was
85-90%) and that corrective fertilization was
applied.

With respect to the successful introduction
of legumes into grasslands receiving more
than 700 mm per annum, it has been found that
with the wide range of species evaluated, the
most successful establishment has invariably
been where a pasture seeder incorporating
cultivation, liming, fertilizer placement,
seeding and compaction was used (Krog, et
al., 1969; Edwards, 1978; Barnes, et al.,
1986). Although persistence of most of the
legumes in such situations is often a
problem, the selection of new cultivars
(Smith & Morrison, 1983) offers a possible
solution.

---

[1]R. H. Drewes-personal communication
[2]G. F. S. Hyam - personal communication
[3]N. F. G. Rethman and G. D. Kotzè -
  unpublished data

LITERATURE CITED

Barnes, D. L., Rethman, N. F. G., de Witt, C.
  C. and Kotzè, G. D. 1986. Exploratory
  trials on reinforcement of veld with
  legumes in the South Eastern Transvaal
  Highveld. J. Grassl. Soc. Sth Afr.
  3.3:90-95.

Cross, G. W. 1978. Conventional methods of
  pasture establishment. Pasture Production
  Manual, Natal Region, Dept. Agric. Tech.
  Services.

Dickinson, E. B., Hyam, G. F. S., Metcalf,
  H. D., Rudert, C. P. and Williams, F. R.
  1984. The pasture handbook. Triomf
  Fertilizer Ltd. Braamfontein, South
  Africa.

Edwards, P. J. 1978. Pasture establishment
  methods: Veld reinforcement and
  replacement. Pasture Production Manual,
  Natal Region, Dept. Agric. Tech.
  Services.

Fair, J. 1986. Guide to profitable pastures.
  M & J Publications, Harrismith, South
  Africa.

Krog, M. M., Theron, E. P. and Andrews, C.
  1969. An experimental sod seeder. Proc.
  Grassl. Soc. Sth Afr. 4, 126-130.

Kruger, J. A., du Toit, P. J., Labuschagne,
  M. J., Niksch, L. A., de Villiers, J. D.,
  Wolfaardt, A. J. and Te Boekhorst, H.
  1985. Guidelines for the production of
  planted pastures. Agric. Devpt.
  Central/West Cooperative, Klerksdorp,
  South Africa.

Rethman, N. F. G. 1973. Eragrostis curvula.
  A review with special reference to
  Southern Africa. Tech. Comm. No. 116.
  Dept. Agric. Tech. Services.

Rethman, N. F. G. and Beukes, B. H. 1973.
  Overseeding of Eragrostis curvula on North
  Eastern Sandy Highveld. Proc. Grassl. Soc.
  Sth Afr. 8, 57-59.

Rethman, N. F. G. 1974. Eragrostis curvula.
  Leaflet No. 119. Fmg. in S. Afr. Dept.
  Agric. Tech. Services.

Rethman, N. F. G. and de Witt, C. C. 1984.
  The production potential of pure and mixed
  stands of Eragrostis curvula and Medicago
  sativa on the Eastern Transvaal Highveld.
  J. Grassl. Soc. Sth Afr. 1.3:30-32.

Rethman, N. F. G. 1985. Smuts fingergrass.
  Information Week Nooitgedacht Res. Sta.
  Dept. Agric. & Water Supply.

Smith, A. and Morrison, A. R. J. 1983. A
  deep rooted white clover for South African
  Conditions. Proc. Grassl. Soc. Sth Afr.
  18: 50-52.

BREEDING FOR IMPROVED SEEDLING ESTABLISHMENT IN
COOL-SEASON RANGE GRASSES

K. H. Asay and D. A. Johnson[1]

ABSTRACT

Heritable genetic variation has been found in
Russian wildrye, crested wheatgrass, and
interspecific hybrids for seedling vigor and other
characteristics associated with stand
establishment on semiarid sites. Seed weight,
emergence from deep seeding, and coleoptile length
have been effective selection criteria for
seedling establishment in these populations.
Crested wheatgrass and Russian wildrye cultivars
with improved capacity for stand establishment
have been developed and released.

INTRODUCTION

Failure to achieve stands of seeded perennial
grasses is a major obstacle in programs to improve
rangelands. Problems are intensified in arid and
semiarid western areas where relatively weak
seedlings of perennial grasses must contend with
environmental stresses of temperature, drought,
and wind; poorly prepared seedbeds; excessive
planting depths; and competition from vigorous
annual weeds. Improved stand establishment is an
objective of most breeding programs with range
grasses. The need for more effective screening
procedures and a better understanding of
environmental and genetic factors associated with
seedling vigor has been well documented (Johnson
1980; Johnson et al. 1981).

Even with effective screening techniques for
seedling vigor, genetic progress will be minimal
if an adequate germplasm base has not been
established. A critical need exists for increased
plant exploration, genetic introgression from
related species, induced polyploidy, and other
means of upgrading the germplasm base from which
improved cultivars are to be extracted.

Some people are convinced that only plant
materials that are native to North America should
be used in range improvement programs. However,
germplasm from introduced sources has had and will
continue to have a major impact on American
agriculture, including western range. The major
concern should be to develop superior plant
materials for specific environments and needs, and
it matters little whether the genetic background
traces to native, introduced, or hybrid
combinations of native and introduced species.
Opportunities for genetic improvement are evident
in both native and introduced populations and
introgression of genetic traits between them is a
realistic objective.

[1]Research Geneticist and Plant Physiologist, USDA-
ARS, Forage and Range Research Unit, Utah State
University, Logan, Utah 84322-6300. Approved as
Journal Paper No. 3386.

This paper emphasizes breeding for improved
seedling establishment in two important cool-
season grasses. Details of the selection
procedures can be found in Johnson and Asay (this
volume).

RUSSIAN WILDRYE

Russian wildrye, Psathyrostachys juncea (Fisch.)
Nevski, has been an important component of
seedings on western rangelands, particularly in
the northern Great Plains of the U.S. and the
adjacent Canadian provinces. Established plants
of Russian wildrye are persistent and productive,
and because of its excellent curing properties,
the species is an excellent source of high quality
forage during the late summer and fall (Lawrence
and Troelsen 1964). Poor seedling vigor has
prevented Russian wildrye from reaching its full
potential. It is difficult to establish,
particulary when subjected to excessive planting
depths, limited soil moisture, blowing soil, and
other adverse environmental conditions. It
follows that improvement of seedling vigor should
be a major breeding objective in this potentially
valuable range grass.

Several reports in the literature have associated
seed weight with seedling vigor, and Kneebone
(1972) concluded in his review that seed size was
the most promising selection criterion available
to a breeder working to improve seedling vigor of
forage grasses. Lawrence (1975) concluded from
his studies of genetic variation in Russian
wildrye that seed weight was controlled to a large
degree by the maternal parent and that additive
genetic effects were instrumental in explaining
genetic variation in number of days to emergence.
His data also suggested that selection in the
seedling stage could have positive benefits on
forage and seed yield of mature plants.

Lawrence (1963) compared several procedures to
evaluate Russian wildrye breeding populations for
improved seedling vigor. He concluded that the
most effective approach would be to eliminate
lines with lighter seed and select from the
remainder, those lines that emerge after to deep
seeding in the greenhouse or field. Speed of
germination also showed some promise as an
important component in a selection index.
Screening for improved seedling emergence and
vigor from deep seedings was instrumental in the
development of 'Swift', an improved cultivar
recently released from the breeding program at
Swift Current, Saskatchewan (Lawrence 1979).
Swift has demonstrated excellent establishment
vigor in several evaluation trials conducted in
the field and greenhouse.

Berdahl and Barker (1984) studied the genetic
variability for seedling vigor and related
characteristics in 30 progeny lines of Russian
wildrye. Mean seed weight of the progenies, which
ranged from 2.1 to 4.5 mg/seed, was significantly
correlated with emergence and coleoptile length,
but the association decreased when seed weight
increased beyond 3.0 mg/seed. Seedling emergence
in two field tests was positively and

significantly correlated with coleoptile length and emergence from a 5 cm planting depth in the greenhouse, but not with emergence under laboratory-induced drought stress. Realized heritability estimates, based on parent-progeny relationships, ranged from 37 to 75% for seed weight and from 52 to 85% for coleoptile length. These estimates suggest that genetic progress for seedling vigor might be achieved by selecting for coleoptile length in populations that have previously been screened for seed size.

Asay and Johnson (1980) screened 134 progeny lines of Russian wildrye for several characteristics associated with seedling vigor in the greenhouse and field. The progenies were from clones selected from a large source nursery largely on the basis of mature plant characteristics. Significant (P < 0.01) differences were found among progenies in greenhouse trials for total emergence and rate of emergence from a 7.6 cm planting depth, and in subsequent height and dry matter yield of seedlings. Broad-sense heritability values ranged from 52 to 70% for these estimates of seedling vigor in the greenhouse. Asay and Johnson also detected significant genetic variation for seedling vigor among the progeny lines in the field trials. The variance and range among progenies for seedling emergence and for percent stand in the fall were particularly encouraging. Emergence ranged from 8 to 120 seedlings per 1.8 m section of row and stand ranged from 42 to 86%. The genetic variance comprised 56% of the phenotypic variance for emergence and 35% for stand establishment. A significant but low correlation (r = 0.30) between seedling emergence in the spring and percent stand in the fall indicated that progenies differed in seedling survival and possibly rate of tillering.

A multiple regression analysis revealed that the combined data from all laboratory procedures used by Asay and Johnson (1980) accounted for only 11 to 14% of the variation in emergence and seedling vigor in the field. Seedling emergence from 7.6 cm planting depth and subsequent evaluations of seedling vigor gave the best estimates of performance in the field. Seedling emergence under two levels of artificially imposed drought stress and seedling recovery after drought stress were not correlated with any of the field data.

The relatively poor correlation among characters in the field and between laboratory and field data adds to the complexity of developing an effective selection index for stand establishment. Johnson and Asay (1980) concluded that preliminary screening for seed weight, followed by selection in the field for percent stand in the fall of the establishment year would be the most productive procedure. Percent stand is contingent on several factors including emergence, vigor and survival of seedlings, and tillering capacity.

Clonal lines, selected largely on the basis of progeny performance in trials conducted by Asay and Johnson (1980), were isolated in crossing blocks to compound an experimental strain (Syn-A). A recurrent selection program is in progress with this population to make additional improvements in stand establishment vigor. Data from evaluation trials on representative range sites indicate that substantial progress has been made. On a range site near Lasal, Utah, for example, Syn-A produced 77 and 138% more forage during the seeding year and the first year after seeding, respectively, than the prevalent Russian wildrye cultivar, 'Vinall'. During the same two years at the USU Blue Creek Experiment Station in NW Utah, Syn-A produced 15 and 36% more forage than Vinall. Present plans are to release this experimental strain as a cultivar within two years.

CRESTED WHEATGRASS

Crested wheatgrass (Agropyron spp.) is actually a complex of diploid (2n=2x=14), tetraploid (2n=4x=28), and hexaploid (2n=6x=42) species. The diploid form is represented in North America by Fairway, Agropyron cristatum (L.) Gaertner, and the most common tetraploids are Standard, A. desertorum (Fisch. ex Link) Schultes, and Siberian, A. fragile (Roth) Candargy, (Dewey 1984). The tetraploids are the most prevalent form on rangelands in the U.S., and the diploids are more common in Canada. New sources of diploid germplasm have recently been reported (Dewey and Hsiao 1984) and may be useful in future breeding programs. Hexaploids have been introduced in North America and, although they may eventually be a factor in rangeland improvement, they have not as yet been included in large scale seedings. We have assembled a germplasm base and initiated a breeding program at Logan to develop improved hexaploid cultivars.

Because of difficulty encountered in making interploidy crosses and sterility problems in hybrid progenies, breeders have concentrated largely on selection and hybridization within ploidy levels, primarily the diploid and tetraploid levels. Dewey (1974) concluded that the same basic genome, modified by structural rearrangements, occurs at the three ploidy levels of crested wheatgrass. He advised breeders to treat the species in the complex as a single gene pool. All possible crosses have now been made among the diploid, tetraploid, and hexaploid levels, and several schemes have been devised and tested to effect interploidy genetic transfer (Asay and Dewey 1983).

To date, the most productive procedure has been to stabilize interploidy populations at the tetraploid level. Plant materials derived from hybrids between hexaploids and diploids, hexaploids and tetraploids, and colchicine-induced tetraploids (C4x) and natural tetraploids (N4x) have shown potential for expanding the genetic resources of tetraploid breeding populations (Asay and Dewey 1979, 1983; Dewey 1974; Dewey and Pendse 1968).

In 1974, 8,000 plants of the F_3 C4x-N4x hybrid were included in a 20,000-plant source nursery. Progenies selected from the source nursery were evaluated for seedling vigor on two range sites and in the laboratory according to procedures described by Asay and Johnson (1983). They found

significant (P < 0.01) differences among 170 progeny lines in both field trials for seedling emergence, seedling height, and first-year stands. Seedling emergence averaged over locations ranged from 18 to 84%. The genetic variance comprised 52 and 44% of the phenotypic variance for emergence and stand, respectively. In general, seedling emergence and vigor in the field were poorly correlated with laboratory determinations of seedling emergence under artificially imposed drought stress and seedling recovery after drought stress. As with Russian wildrye, seed weight was significantly (P < 0.01) and positively correlated with all seedling vigor characters evaluated in the field, indicating that preliminary screening for seed weight followed by evaluation of stand establishment under semiarid conditions in the field would be a productive approach.

Over 70% of the crested wheatgrass clones selected from the base population, largely on the basis of seedling vigor, were derived from C4x-N4x hybrids. Three synthetic strains, two from hybrid parentage and one natural tetraploid, were compounded and entered in evaluation trials on several range sites. One of the hybrid strains was released as the cultivar 'Hycrest' in 1984 (Asay et al. 1985b).

Hycrest has demonstrated excellent vigor and productivity during and immediately after stand establishment (Asay et al. 1986). The new cultivar has consistently produced more forage than Nordan and Fairway in field trials, particularly during the early phases of stand establishment and under environmental stress (Table 1).

Table 1. Forage yield of three crested wheatgrass cultivars on five range sites during stand establishment (Yr-1) and subsequent seasons, Yr-2 and Yr-3 (From Asay et al. 1986).

	Location			
	A[1]	B	C	
Cultivar	Yr-1	Yr-1	Yr-2	Yr-3
			kg/ha	
Hycrest	4090	1340	2610	2050
Nordan	3790	480	1550	1500
Fairway	3630	630	960	1400
LSD (0.05)	550	120	390	250

1/ Locations: A, Decker, Montana, annual precipitation 31.8 cm; B, Blue Creek, NW Utah, annual precipitation 36.6 cm; and C, Lakeside, Utah, annual precipitation 15.4 cm.

This is exemplified in trials at Lakeside, Utah, near the Bonneville salt flats. This is a harsh site with 15.4 cm annual precipitation and a heavy infestation of halogeton, Halogeton glomeratus (M. Bieb.) C. Meyer, and cheatgrass (Bromus tectorum L.). Excellent stands of Hycrest were obtained with no herbicide application, and by the second year, both weed species were essentially eliminated in the Hycrest plots. During the first year after stand establishment, forage yields were 2,610, 1550, and 960 kg/ha for Hycrest, Nordan, and Fairway, respectively. Corresponding herbage yields for the next year were 2,050, 1,500, and 1,410 kg/ha.

On a surface mine reclamation site (A) near Decker, Montana, where moisture conditions were near optimum during the year after seeding, excellent stands were obtained for all crested

wheatgrass entries. Although Hycrest produced more forage than Nordan or Fairway, the differences were considerably less than under drought stress at Lakeside. Herbage yields during the first year after seedling establishment were 4,090, 3,790, and 3630 kg/ha for Hycrest, Nordan, and Fairway, respectively. Evaluations to date indicate that Hycrest has heavier seeds than other crested wheatgrass cultivars.

SEEDLING VIGOR-DROUGHT STRESS INTERACTIONS

We have incorporated a line-source irrigation system to study the interactions between stand establishment characteristics and drought stress in range grasses and alfalfa (Asay and Johnson 1986; Rumbaugh et al. 1984). Initially, seedling vigor of 20 progeny lines of the RS hybrid

[Elytrigia repens (L.) Nevski] X Pseudoroegneria spicata (Pursh) Love] was studied at 10 levels of available soil moisture. In general, significant differences were found among the progeny lines for seedling emergence, stand counts, and seedling dry matter yields. The magnitude of the differences, however, declined substantially as drought stress was increased. The genetic variance among progeny lines reached a maximum at optimum moisture levels and declined in a curvilinear manner to near zero at extreme levels of stress.

Expected genetic advance at the different levels of drought stress plus data on the relative performance of the progeny lines at each of the stress level, suggested that selection for seedling vigor in the RS hybrid would be most effective at intermediate moisture levels between optimum and extreme stress. The line-source sprinkler system, whether used in the field or greenhouse, allows the breeder to accurately define the level(s) of drought stress to impose during the screening process. Data from more than one drought-level segment can be considered or the length of the various segments can be adjusted for additional flexibility.

LITERATURE CITED

Asay, K. H. and D. R. Dewey. 1979. Bridging ploidy differences in crested wheatgrass with hexaploid X diploid hybrids. Crop Sci. 19:519-523.

Asay, K. H. and D. R. Dewey. 1983. Pooling the genetic resources of the crested wheatgrass species-complex. J. A. Smith and V. W. Hays (eds.). Proc. Int. Grassl. Cong., Lexington, KY. 15-24 June 1981. 14:124-127.

Asay, K. H., D. R. Dewey, F. B. Gomm, W. H. Horton, and K. B. Jensen. 1986. Genetic progress through hybridization of induced and natural tetraploids in crested wheatgrass. J. Range Manage. 39:261-263.

Asay, K. H., D. R. Dewey, F. B. Gomm, D. A. Johnson, and J. R. Carlson. 1985a. Registration of Bozoisky-Select Russian Wildrye. Crop Sci. 25:575-576.

Asay, K. H., D. R. Dewey, F. B. Gomm, D. A. Johnson, and J. R. Carlson. 1985b. Registration of Hycrest crested wheatgrass (Reg. No. 16). Crop Sci. 25:368-369.

Asay, K. H. and D. A. Johnson. 1980. Screening for improved stand establishment in Russian wild ryegrass. Can. J. Plant Sci. 60:1171-1177.

Asay, K. H. and D. A. Johnson. 1986. Drought and seedling vigor responses in perennial Triticeae grasses. Agron. Abstr. p.55-56.

Asay, K. H. and D. A. Johnson. 1983. Genetic variability for characters affecting stand establishment in crested wheatgrass. J. Range Manage. 36:703-706.

Berdahl, J. D. and R. E. Barker. 1984. Selection for improved seedling vigor in Russian wild ryegrass. Can. J. Plant Sci. 64:131-138.

Dewey, D. R. 1974. Reproduction in crested wheatgrass pentaploids. Crop Sci. 14:867-872.

Dewey, D. R. 1984. The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. p. 209-279 In: J. P. Gustafson (ed.). Gene Manipulation in Plant Improvement. Plenum, New York.

Dewey, D. R. and C. I. Hsiao. 1984. The source of variation in tetraploid crested wheatgrass. Agron. Abstr. p.64.

Dewey, D. R. and P. C. Pendse. 1968. Hybrids between Agropyron desertorum and induced-tetraploid Agropyron cristatum. Crop Sci. 8:607-611.

Johnson, D. A. 1980. Improvement of perennial herbaceous plants for drought-stressed western rangelands. In: N. C. Turner and P. J. Kramer (eds.). Adaptation of Plants to Water and High Temperature Stress. John Wiley & Sons. Inc. New York.

Johnson, D. A., M. D. Rumbaugh, and K. H. Asay. 1981. Plant improvement for semiarid rangelands: Possibilities for drought resistance and nitrogen fixation. Plant and Soil 58:279-303.

Kneebone, W. R. 1972. Breeding for seedling vigor. p. 90-100. In: C. M. McKell and V. B. Youngner (eds.). The Biology and Utilization of Grasses. Academic Press, New York.

Lawrence, T. 1963. A comparison of methods of evaluating Russian wild ryegrass for seedling vigor. Can. J. Plant Sci. 43:307-312.

Lawrence, T. 1975. Genetic control of variation in a selected population of Russian wild ryegrass (Elymus junceus). Can. J. Plant Sci. 56:275-280.

Lawrence, T. 1979. Swift, Russian wild ryegrass. Can. J. Plant Sci. 59:515-518.

Lawrence, T. and J. E. Troelsen. 1964. An evaluation of 15 grass species as forage crops for southwestern Saskatchewan. Can. J. Plant Sci. 44:301-310.

Rumbaugh, M. D., K. H. Asay, and D. A. Johnson. 1984. Influence of drought stress on genetic variances of alfalfa and wheatgrass seedlings. Crop Sci. 24:297-300.

SELECTION FOR IMPROVED ESTABLISHMENT IN
WARM-SEASON GRASSES

P. W. Voigt, C. R. Tischler and B. A. Young[1]

ABSTRACT

Establishment of warm-season perennial grasses is
frequently difficult. Genetic variation exists
within primary gene pools for numerous
characteristics related to plant establishment
and selection progress has been demonstrated for
many of them. A major effort is needed to select
for multiple establishment characteristics in
important species.

INTRODUCTION

Improving establishment ability has been a
concern of grass breeders in the western U.S. for
many years. Kling Anderson at the third meeting
of the Western Grass Breeders Work Planning
Conference (GBWPC) suggested that seedling vigor
could be improved by, ". . . Beginning selection
with seedlings started in dense populations and
under adverse conditions," (Anon 1949).
Discussion by the group of 24 in attendance at
that meeting in Logan, Utah "showed widely
varying thoughts on such phrases as what is
seedling vigor and how do we recognize it?"
Certainly that diversity of opinion is
represented in the work reported in this paper.

The difficulty of establishing warm-season
grasses is well known. Because of their
requirement for warm temperatures, warm-season
grasses are usually planted when environmental
conditions are more severe than when cool-season
grasses are planted. Thus, warm-season grass
plantings are thoroughly exposed to the hazards
described by Jack Harlan at the fourth meeting of
the GBWPC (Harlan 1950). "Among these may be
counted drouth, torrential rains, washing, wind
erosion, sand blast, unseasonable frosts, baking
and crusting of the soil, hail, insects,
diseases, and competition from other plants."
The need for improved plant establishment through
breeding as well as management practices is just
as true now as it was then. Although progress
has been made, even more progress is required.
This paper will review reports of genetic
variation in establishment and related
characteristics of warm-season grasses that could
be exploited in conventional plant improvement
programs, primarily intraspecific variation, and
results that have been obtained from selection
attempts. We will emphasize perennials although
work with annuals will not be excluded. L. Neal
Wright (1971c) wrote an excellent review from a
somewhat wider perspective. We will not consider
salt or herbicide resistance.

[1]Research Geneticist, Plant Physiologist, and
 Research Geneticist, respectively, USDA - ARS,
 Grassland, Soil and Water Research Laboratory,
 PO Box 6112, Temple, Texas 76503-6112.

CARYOPSIS SIZE

The existence of a relationship between caryopsis
(seed) size and vigorous seedlings has been
accepted by most grass breeders. Kneebone and
Cremer (1955) demonstrated the effect of genetic
and nongenetic differences in seed size on
seedling vigor of several warm-season grasses.
Endosperm size appears to be the primary reason
for this increase in growth. Reducing the amount
of endosperm, by removing part of it, decreased
root and shoot growth of corn (Zea mays L.)
(Cooper and MacDonald 1970). High sugar
genotypes of sweet corn are well known for their
small seed and poor seedling vigor and
establishment (e.g., Rowe and Garwood 1978).
Wann (1980) found that excised embryos of high
sugar and normal genotypes had similar vigor when
grown on agar. The larger endosperm of larger
seeds supplies additional energy for early growth
and for rapid development of leaf area.

Variation in seed size has been reported for many
perennial warm-season grasses (Table 1). We have
been somewhat conservative in compiling this list
and have not included examples where differences
in seed size may have been caused by
environmental rather than genetic variation.
Clearly, genetic variation for seed size is wide
spread and can probably be found in all grasses.
Thus, it is somewhat surprising that there have
been few serious attempts to capitalize on this
variability (Table 1).

Table 1. Variation for caryopsis size in warm-
season perennial grasses.

Species	Reference
Intraspecific variation:	
Andropogon gerardii[1]	Kneebone 1956
	Boe and Laposky 1983
	Glewen and Vogel 1984
Bothriodhloa ischaemum	Coyne and Bradford 1985
B. bladhii	Coyne and Bradford 1985
Bouteloua curtipendula	Kneebone and Cremer 1955
	Kneebone 1956
	Major and Wright 1974
B. gracilis	Wilson et al. 1981
Buchloe dactyloides	Kneebone 1956
Eragrostis lehmanniana	Wright and Brauen 1971
Panicum antidotale	Wright 1971a
P. coloratum	Potts and Holt 1967
P. virgatum	Nielsen 1944
	Kneebone 1956
	Boe and Johnson 1987
Pennisetum purpureum	Pearson 1975
Sorghastrum nutans	Kneebone 1956
	Barnett and Vanderlip 1969
Successful selection:	
Bouteloua gracilis	Wilson et al.[2]
Panicum antidotale	Wright 1976
Panicum coloratum	Hussey and Holt 1986

[1]Scientific names follow Terrell et al. 1986.
[2]Wilson, Cuany, Fraser and Oaks, unpublished.

One objection to selecting for larger seed is the possibility that an increase in the seed size component of seed yield could result in reduction of another component, seed number (e.g., Moore and Cavers 1985). Wilson et al. (1981) have suggested that, based on their data, it should be possible to select for both seed size and seed yield in blue grama, Bouteloua gracilis (Willd. ex Kunth) Lagasca ex Griffiths. It may be that seed size can be increased without adversely impacting seed yield. Abernathy and Wright (1975) reported a positive association between increased photosynthetic efficiency and increased seed mass.

The effect of selection for increased seed mass on performance of warm-season perennial grasses has not been well documented. Wright (1977), working with blue panicgrass, Panicum antidotale Retz., compared the performance of five clones each from the fifth cycle of divergent recurrent selection for heavy and light seed mass. He found that seedlings grown in controlled environment conditions from the heavy seed clones were consistently superior in root and shoot growth to seedlings from the light seed clones. Differences in growth were observed from early seedling stages to 54-day-old plants. The initial advantage provided by the heavy seed was maintained throughout the experiment. In later work, Abernathy et al. (1977) found that germinating seeds from the heavy seed clones had higher respiration rates (first 72 hr) and contained more free sugars and greater pools of adenylate phosphates than seeds from the light seed clones. Divergent selection for seed mass had resulted in significant differences in germination and seedling growth. Unfortunately, the clones used for the study were the extreme genotypes from the fifth cycles rather than a random sample. Thus, the results obtained cannot be said to characterize those cycles. Also, the original population was not included in the study. An accurate estimate of progress from selection cannot be made. Abernathy and Wright (1975) reported that inflorescences of clones from the sixth cycle high seed mass population had higher apparent photosynthesis and lower dark respiration than clones from the low seed mass population.

The effect of increased seed mass on seedling characteristics of kleingrass, Panicum coloratum L., has not been adequately reported[2]. Data suggests that a significant increase in seedling mass resulted from selection for increased seed mass but that rooting characteristics were not affected. The first cycle population was released as 'Verde.'

An experimental strain of blue grama was developed through three cycles of selection--primarily for seed mass but secondarily for emergence from deep planting and shoot and root growth[3]. Although accurate comparisons among cycles in single experiments have not been reported, the gains in seed mass are sufficient to show that excellent progress has been made. Work with seed from selected clones of the base population suggests that increased seed mass in blue grama is associated with increased emergence from deep planting, increased shoot weight and increased adventitious root weight (Carren et al. 1987a, 1987b).

SEED DORMANCY AND GERMINATION RATE

The value of seed dormancy as it affects establishment is controversial. Many would probably agree with Jack Harlan (1950) that in seeding a new stand, "A substantial proportion of hard seed is good insurance." Yet others have found that, at least in a more humid environment like eastern Kansas, "Variation in spikelet germination prior to dormancy reducing treatment satisfactorily accounted for significant progeny differences in establishment. . ." (Barnett and Vanderlip 1969). In other words, the dormant seed was of little or no value in stand establishment of Indiangrass, Sorghastrum nutans (L.) Nash. Yet dormant seed was probably of the greatest importance in long term persistence when a hot June fire killed 98% of a lehmann lovegrass, Eragrostis lehmanniana Nees, stand (Cable 1965). Because heat desiccation is known to break seed dormancy in 'A-68' (common) lehmann lovegrass (Haferkamp and Jordan 1977) it seems likely that the hot June fire broke the dormancy of seed shattered onto the soil surface in earlier years. Before the end of that same summer, the density of new lovegrass plants was six times that of the original stand. Weaver and Jordan (1985) have shown that heat desiccation can also increase the rate of germination of A-68. Possibly dormancy of some genotypes may be associated with reduced speed of germination. Chances of successful establishment could be reduced unless seeds were heat treated prior to planting or soil temperatures were high enough to break dormancy. Clearly, seed dormancy can have both positive and negative effects on stand establishment and persistence.

Variation in seed dormancy has been reported in many warm-season grasses (Table 2). Similarly, variation has been reported also in response of different genotypes to heat desiccation treatment, e.g., Eragrostis curvula (Schrader) Nees (Weaver and Jordan 1985) and Digitaria milanjiana (Rendle) Stapf (Hacker 1984). In the latter case, the ecotypes that responded to heat desiccation with improved germination were from arid locations with widely varying seasonal climates. Ecotypes from wet locations or dry equatorial locations did not have that kind of dormancy. The value of seed dormancy to species establishment and/or persistence may vary with the climate.

---

[2]Hussey and Holt, unpublished; Tischler, Voigt and Holt, unpublished.
[3]Wilson, Cuany, Frazer and Oaks, unpublished.

Table 2. Variation in seed unit dormancy in warm-season perennial grasses.

Species	Reference
Intraspecific variation:	
Bothriochloa ischaemum	Ahring and Harlan 1961
Bouteloua curtipendula	Major and Wright 1974
Digitaria milanjiana	Hacker 1984
Eragrostis lehmanniana	Wright and Brauen 1971
Panicum maximum	Smith 1979
Schizachyrium scoparium	Coukos 1944
Sorghastrum nutans	Barnett and Vanderlip 1969
Successful selection:	
Panicum coloratum	Tischler and Young 1987

Variation reported for seed dormancy and seed size in lehmann lovegrass (Wright and Brauen 1971) must be viewed with caution because of the unsettled status of taxonomy in the germplasm related to the apomictic complex that includes E. curvula and E. lehmanniana. Samples regarded as lehmann lovegrass by Neal Wright were identified as either E. curvula or E. barbinodis Hack by the Royal Botanic Gardens at Kew[4]. Also, plotting of the seed dormancy and seed mass data (Wright and Brauen 1971) reveals a discontinuity in the distributions (fig. 1). Based on growth habit the selections were divided into two types, bunch (B) or stolon (S). The diversities in seed dormancy and seed mass and the discontinuity occur in the bunch group. Dormancy within the group ranges from 0 to 100% while seed mass ranges from 8 to 27 mg/100 seeds. It appears possible that at least some of the B group should be referred to the cold-hardy lehmann type (CHL) that has been traditionally identified as E. lehmanniana in the U.S. In other parts of the world, the CHL type has been more commonly referred to E. curvula. The only cultivar of that type 'Cochise' has been designated in the U.S. as E. lehmanniana Nees x E. trichophora Coss and Dur. (Holzworth 1980). Hybridization research[5] suggests that it might more properly be referred to E. curvula than to E. lehmanniana. This suggestion is in agreement with the Kew analysis of Neal Wright's specimens. The correspondence and my notes indicate that only bunch specimens were sent to Kew. However, seed mass of CHL strains can vary (Table 3), from a mass similar to boer lovegrass to a mass similar to A-68 lehmann lovegrass.

Seed dormancy of Lacy and Cochise has not been reported. If the discontinuity represents a real difference rather than a gap in sampling, the negative relationship between seed mass and dormancy reported by Wright and Brauen (1971) must be disregarded. If the discontinuity results from inadequate sampling then the relationship may be correct. In either case, it appears likely that the relationship should not be ascribed to "true"

[4]Letter from Sir George Taylor to Dr. L. Neal Wright.
[5]Voigt and Burson, unpublished.

lehmann lovegrass which shows no appreciable variation in either seed mass or seed dormancy.
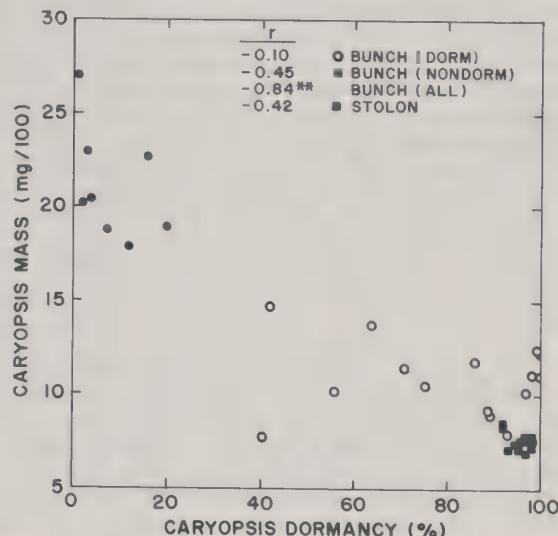

Figure 1. Distribution of caryopsis mass and dormancy in "lehmann" lovegrass (Wright and Brauen 1971)

Table 3. Seed mass of lovegrass strains.

Grass	Strain	Mean[1]	SD
		mg/100 seeds	
Lehmann	A-68	8.6	0.15
Boer	A-84	16.2	0.51
	Catalina	14.8	0.26
CHL	Cochise	10.5	0.36
	Lacy[2]	18.4	0.50
Weeping	Ermelo	32.5	0.35

[1]Mean of three determinations.
[2]Experimental selection.

Successful selection for reduced seed dormancy was conducted in kleingrass (Tischler and Young 1987) but has not been documented in other warm-season grasses.

Wright (1978a) successfully selected for germination rate in blue panicgrass. The means of the sixth cycles for days to 50% germination were 5.5 and 13.8 days for the fast and slow populations, respectively. The response of blue panic seedlings to this increase in germination speed is difficult to interpret because neither the base population nor the final cycles of selection were evaluated. Seed from selected extreme clones of the fast germinating population produced seedlings with longer shoots and roots and greater seedling mass than seed from selected extreme clones of the slow germinating population (Wright 1980).

OSMOTICA

The use of osmotica, e.g., D-mannitol or polyethylene glycol, to simulate drought stress has been widely practiced. Germination and early seedling growth differences among genotypes of warm-season grasses such as switchgrass, Panicum virgatum L.; sideoats grama, Bouteloua curtipendula (Michaux) Torrey; and sand bluestem, Andropogon gerardii var. paucipilus (Nash) Fern., in the presence of varying concentrations of D-mannitol have been reported (Kneebone 1957). Wright (1971a) also reported genetic differences in blue panic germination in the presence of D-mannitol and conducted selection at two different concentrations. Results of the selection were never reported.

A major problem with most work done with osmotica is the direct contact between the osmotica and the germinating seed or growing seedlings. Osmotica could have a specific effect on growth independent of water potential. The effects of drought stress are confounded with the direct effect of the osmotica (Johnson and Asay 1978).

Although techniques have been developed to overcome the problem of seed osmotica contact (Watt 1974, Johnson and Asay 1978), the new procedures have not been used to evaluate intraspecific variation in warm-season grasses. It can be argued, however, that it is not desirable for warm-season grasses to germinate at too low a water potential. Watt (1974) found that warm-season grass species that germinated at the lowest moisture potentials were the "poorest establishers." Compounding the problem, rates of germination are reduced at low water potentials. Silcock (1980) suggested, "A rapid rate of germination and growth would be invaluable to most species, provided seeds did not germinate after unrealistically small falls of rain." Cloudy conditions and/or high humidity following rain (Silcock 1980, Frasier et al. 1987) are usually needed for successful germination and emergence of warm-season grasses in hot arid environments. Germination following an isolated shower can result in failure to emerge.

TEMPERATURE

Although considerable work has been conducted with warm-season annuals, e.g., corn, McConnell and Gardner (1979) and Eagles (1982), little information has been published on intraspecific variation in temperature response of warm-season perennial grasses. Differential response to germination temperatures has been reported in buffelgrass, Cenchrus ciliaris L. (Pandeya and Pathak 1978) desert saltgrass, Distichlis spicata subsp. stricta (Torrey) Thorne, (Cluff et al. 1983) and the E. curvula complex (Martin and Cox 1984). Voigt[6] observed differences in germination of sideoats grama caryopses (Table 4). The apomict 'Tucson' germinated more slowly and less completely than the apomictic

[6]Voigt, unpublished.

selection Hope or the sexual selection Block E at an alternating temperature of 13/18°C. At 30/35°C all three germinated over 97 percent. Hope was slower to germinate at the cooler temperature than Block E but total germination of the two did not differ. Block E had a wider range of temperatures at which it could germinate than the two apomicts. The uniform apomicts appeared to have more restrictive temperature requirements than the sexual Block E.

Table 4. Germination of sideoats gramas at different temperatures.

Temperature	Strain		
	Hope	Tucson	Block E
	——————— % ———————		
	Total germination		
7–13°C	0	0	29
13–18°C	89a[2]	39b	92a
29–35°C	98a	99a	97a
35–41°C	73a	89a	91a
	Speed of germination[1]		
13–18°C	19b	3c	48a
29–35°C	40b	62ab	80a
35–41°C	41a	55a	59a

[1]Germination of first counting day.
[2]Means within a row followed by the same letter are not significantly different at the 0.05 probability level.

EMERGENCE AND SEEDLING SIZE

Most studies concerned with intraspecific variation in establishment of warm-season perennial grasses have considered emergence along with other plant characteristics such as seedling size or final plant counts. Cox and Martin (1984) found that 'Catalina' was superior to 'A-84' boer lovegrass, E. curvula var. conferta Nees, in emergence from three different soils. Cochise was intermediate.

Voigt and Brown (1969) demonstrated significant improvement in seedling establishment in sideoats grama following three cycles of recurrent selection for vigorous seedlings from field plantings. Seedling height was increased also in most evaluation studies.

Selection for vigorous seedlings in more controlled environments has been suggested as another way to improve establishment. Glewen and Vogel (1984) studied both seed and seedling mass in sand bluestem. They found that almost half the genetic variability for seedling mass was due to variation in seed mass. Selection for seedling mass by indirect selection for seed mass would have resulted in expected gains from selection almost as large as those for direct selection for seedling weight. However, genotypes selected by the two techniques would not have been identical. Young and Tischler[7] selected for 14-day shoot mass in kleingrass (fig. 2). The increase in shoot mass

was 23% in one population and 64% in another. Although all the seed mass data for population 1 is not strictly comparable, we have sufficient confidence in the data to suggest that the increase in seedling mass has been achieved without any appreciable effect on seed mass. Data reported by Hussey and Holt (1986) on three cycles of selection for seed mass in kleingrass is included for comparison.
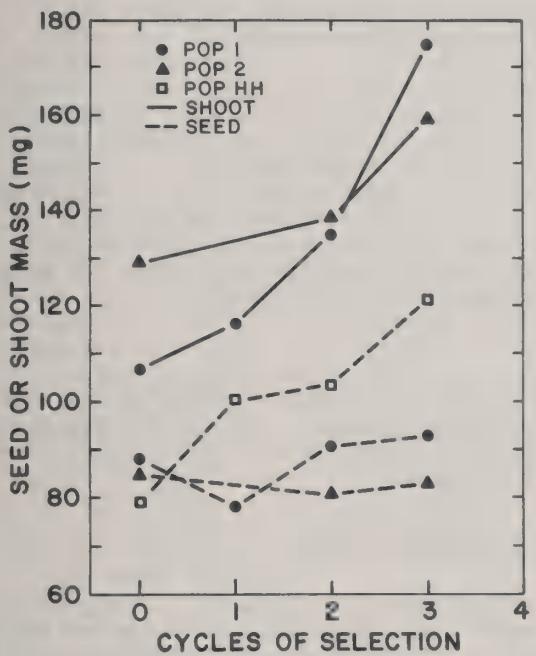

Figure 2. Result of three cycles of selection for high shoot (POP 1 & 2) and seed (POP HH; Hussey and Holt 1986) mass on shoot and seed mass.

Clearly, selection for either seed mass or seedling mass can result in increased seedling vigor. Both approaches appear valid. Is there a difference between them? Selection for increased seed mass is the simpler procedure, and larger seed size has the potential advantage of increasing the value of some seeds such as kleingrass for feed for wild birds (Holt et al. 1985). Increased energy reserves for the developing seedling have usually been considered the primary benefit of increased seed mass (Wright 1971c). What is the physiological basis of increased seedling mass when energy reserves have not been increased? The mechanism could be a faster rate of starch mobilization and/or a higher quality endosperm with a greater protein or phosphorus content (Tischler and Voigt 1983). Because selection for seed mass and for shoot mass per se can capitalize on different mechanisms and different genetic variation, it appears of great importance and value to use both approaches to achieve greater improvement in establishment ability.

---

[7]Young and Tischler, unpublished.

SHOOT DEVELOPMENT

The importance of the subcoleoptile internode (SCI) and coleoptile to emergence and eventual establishment of warm-season grasses is well known. Genetic variation in length of SCI and coleoptile have been reported in rice, Oryza sativa L. (Turner et al. 1982, Takahashi 1978). Recently, Carren et al. (1987a) have reported small differences in coleoptile length and SCI mass per unit length in blue grama primarily associated with differences in seed mass.

Variation in seedling leaf and stem development among switchgrass cultivars was reported by Perry and Moser (1975) Fulbright et al. (1985) have shown that seedlings of PMK-1483 blue grama had a greater leaf blade area and seedling mass than seedlings of PMK-1482. However, Wilson et al. (1981) showed that PMK-1483 had a larger seed mass than PMK-1482. The difference in leaf area and seedling mass could be explained at least in part by the difference in seed mass.

Coyne and Bradford (1985) conducted a detailed study of seedling development in 12 apomictic Old World bluestems, Bothriochloa sp., at two levels of moisture. An attempt was made to minimize the effect of seed size, rate of germination and other seed related factors on seedling characteristics by eliminating light seeds through pneumatic air separation, staggering germination of seed lots and selecting uniformly germinating seeds for transplanting into each pot. Significant differences among Old World bluestems were detected for plant biomass, tiller number, leaf number, leaf blade area and seedling height. The authors suggested that parameters with high sensitivity to water stress would be desirable selection criteria for identification of genotypes with superior stress performance because the required accuracy of the measurements would be less than for parameters of low stress sensitivity. Both plant biomass and leaf blade area were considered potentially useful screening parameters. Coyne and Bradford also reported the variability in seed mass of the 12 genotypes. They ranged from 35.3 to 56.8 mg/100 seeds. Our regression analysis of their seedling characteristics on seed mass data suggests that, despite the effort to minimize effects of seed characteristics on seedling development, three of the characteristics studied--plant biomass, leaf blade area and plant height--were significantly (0.10 probability level) affected by seed mass in the wet treatment (Table 5). Significant relationships were not observed for the dry treatment. The relationships could usually be improved by deleting one or two outlying observations. For example, 'Ganada' was an outlier for both plant biomass and leaf blade area (wet treatment). Coyne and Bradford noted the poor performance of the two Caucasian bluestems in the dry treatment. Even though removing them from the data set resulted in a significant relationship between seedling biomass and seed mass in the dry treatment, the slope of the regression was less than in the wet treatment. Regression analyses suggest that seed mass had its greatest influence on seedling

development in the wet treatment. Under less optimum conditions, the influence of seed mass was reduced. Thus, seed mass may be a poorer predictor of establishment performance in arid than in more optimum environments. However, one must remember that the effect of seed mass in this study would probably have been larger if treatments had been staged from seed planting rather than from transplanting of germinated seed.

Table 5. Linear regression of plant characteristics on caryopsis mass[1].

Character	Trt	N	Slope	F	Prob	R^2
Plant biomass:	Wet	12	0.0030	3.17	0.10	0.24
		11[2]	0.0039	6.44	0.03	0.42
		10[3]	0.0038	10.60	0.01	0.52
	Dry	12	0.0005	0.27	0.62	0.03
		10[4]	0.0020	5.38	0.05	0.40
Leaf blade area:	Wet	12	0.2061	6.00	0.03	0.37
	Dry	12	0.0256	0.19	0.67	0.02
Plant height:	Wet	12	0.2243	3.94	0.08	0.28
	Dry	12	0.0636	0.56	0.47	0.05

[1]Calculated from Coyne and Bradford 1985.
[2]B. ischaemum WW604 deleted.
[3]B. ischaemum WW604 and Ganada deleted.
[4]B. bladhii WW442 and 765 (Caucasian bluestems) deleted.

ROOT DEVELOPMENT

The single seminal root of warm-season perennial grasses has not been extensively studied. Briske and Wilson (1977) did report differences among genotypes of blue grama in seminal root weight. Perhaps more important was the finding of significant differences in water uptake (Wilson and Sarles 1978) among blue grama strains confined to their seminal roots. They reported a north to south trend for increased water uptake in blue gramas from Nebraska to Texas. Differences in water uptake could be related to root anatomy. In rice genotypes, main xylem vessels of seminal roots ranged from 29 to 57 micrometers[8].

Nason et al. (1987) selected for maximum water uptake in blue grama seedlings confined to their seminal roots. Maximum water uptake and shoot mass were determined on seedlings that had reached a plateau or ceiling in the amount of live shoot that could be supported by the water supplying capacity of the seminal root. Shoot mass of plants was also considered in making selections. Shoot mass of plateaued seedlings was increased 21% by two cycles of recurrent selection. Shoot mass was correlated with water uptake (r=0.81**) and caryopsis mass (r=0.40**). The authors suggested that larger populations could be screened if shoot mass of

plateaued seedlings rather than water use was the selection criteria because it was much easier and faster to determine shoot mass than water uptake.

Information has been developed also on adventitious root growth. Voigt and Adams (1977) found that CHL selections of Eragrostis curvula had higher adventitious root growth rates than boer, weeping or boer x weeping hybrids. Wilson (1981) reported differences in adventitious root growth among seedlings of PMT-1482, PMT-1483, Lovington and Hachita blue gramas. The New Mexico origin strains had more adventitious roots and there was a north to south trend for greater total root weight and greater adventitious root elongation. Earlier studies (Briske and Wilson 1977) had documented also blue grama strain differences in length and weight of adventitious roots. Wilson (1981) suggested that a significant strain by temperature interaction for leaf blade length and weight of adventitious roots resulted from the effect of natural selection for seedling vigor at high temperatures in the southern strains. He suggested that because leaf blade length had accounted for 63% of the variation in rate of root elongation selection should be for a general increase in seedling vigor, including high rates of adventitious root growth. O'Toole[8] found also differences in xylem area of adventitious roots and documented their positive effect on water potential of rice plants.

SEEDLING DROUGHT SURVIVAL

Neal Wright conducted extensive seedling drought tolerance (SDT) studies in controlled environment chambers set to mimic natural conditions of temperature and humidity in the arid southwestern U.S. (Wright 1971c). His pioneering work in this area was focused on three grasses: boer lovegrass, lehmann lovegrass and blue panic. In both boer (Wright and Jordan 1970) and lehmann lovegrass (Wright and Brauen 1971), he reported significant differences in seedling survival among apomictic selections. Because of questions concerning the true taxonomic identity of the genotypes studied as lehmann lovegrass, we have plotted the relationship between seed mass and seedling survival (fig. 3). Wright and Brauen's data indicate that there were significant differences in survival among stolon genotypes although there were larger differences among bunch genotypes. However, there was no relationship between seed mass and seedling survival unless all bunch types, regardless of seed mass, were considered together. It does not appear safe to conclude that selection for small seed mass or seed dormancy would be of much benefit to increasing seedling drought survival. The sample size of the larger seeded bunch types is too small to reliably conclude that "lehmann-like" genotypes with that size of seeds will not be seedling drought tolerant.

Wright's results with blue panic were never completely described. A preliminary report suggests that some progress may have been made (Wright 1975). The survival percentage of the sixth cycle ranged from 3.1 to 15.1 with a mean of 7.3. Unselected blue panic had a mean of 5.3.
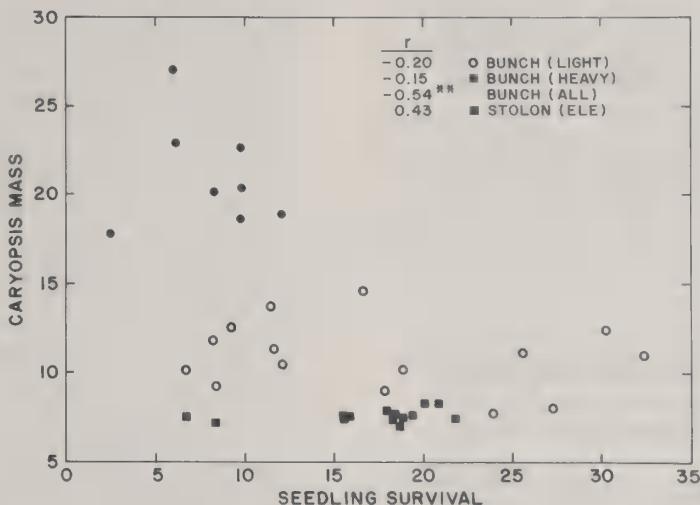
[8]O'Toole et al., unpublished.

Figure 3. Distribution of caryopsis mass and seedling drought tolerance in lehmann lovegrass (Wright and Brauen 1971).

Wright's work resulted in the release of three cultivars: 'Catalina' boer lovegrass (Wright 1971b) and 'Kuivato' and 'Puhuima' lehmann lovegrass (Wright 1978b). The latter two cultivars are the most dormant (fig. 1) and seedling drought tolerant (fig. 3) of the bunch type genotypes studied by Wright and Brauen (1971). The SDT blue panic was never released.

Studies were conducted in all three grasses to search for other characteristics that would relate to their SDT. In blue panic, there was no relationship between SDT and water use efficiency (Dobrenz et al. 1969a), but SDT was negatively related to mean stomatal density (Dobrenz et al. 1969b). In boer lovegrass, SDT correlated only with water use, but the genotypes that had the most SDT also had the highest water use (Wright and Dobrenz 1970). In "lehmann lovegrass" genotypes with the most SDT were the most water-use-efficient and also had the highest content of petroleum ether extract (Wright and Dobrenz 1973). Hull et al. (1978) observed differences in wax structure between genotype extremes in SDT. In each of these studies, only a few extreme genotypes were compared. The differences reported show no consistency from species to species. They provide no consistent guideline on which to predict or to select for seedling drought survival.

Variations in other characteristics that should relate to seedling survival have been reported. Wilson and Sarles (1978) observed differences among blue grama strains in leaf diffusion resistance. Other characteristics of obvious importance have been discussed earlier.

Catalina has been the most successful of the SDT selections. In field (Wright and Jordan 1970, Cox et al. 1986) and greenhouse (Frasier et al. 1985) studies, it has given good performance in initial field establishment. Catalina has also persisted relatively well compared to other lovegrasses

(Cox and Jordan 1983, Cox et al. 1986). Kuivato and Puhuima, L-38 and L-28, respectively, have not done as well. Kuivato showed some promise in establishment but did not establish as well as A-68 lehmann lovegrass (Cox and Jordan 1983). Following planting in 1970, Kuivato did show an increase in stand between 1970 and 1971, apparently a reflection of its high seed dormancy. Although long term persistence has not been as good as desired, one should remember that selections were made on the basis of seedling, not mature plant, drought tolerance. There is no reason to assume that SDT will be a perfect predictor of mature plant drought tolerance.

SEED LOTS

You may not see how the subject of seed lots relates to the overall topic of this paper, but it does, and in the same way that it relates to many of the other papers in this symposium. Most, if not all of us, have examined the response of a single seed lot of a cultivar or experimental selection to an environmental variable and then concluded that the response we observed was a function of that genotype. Of course we were correct, but perhaps only partly so. We may have been measuring the effect of environment on the maturing seed, the maturity of the seed when it was harvested, the harvesting and processing procedures used, the age of the seed, the conditions under which the seed was stored, or a host of other factors. To accurately characterize the response of a genotype, not only the treatment but the seed lot must be replicated, or genotype and seed lot will be confounded. Even when we use replicated seed lots we must be able to assure ourselves and our readers that we are working with high quality seed that will allow the potential of the genotype to be expressed.

Year of harvest had a major effect on dormancy in different apomictic genotypes of _Bothriochloa ischaemum_ (L.) Keng. (Table 6) (Ahring and Harlan 1961). Needless to say, the genotype by seed harvest year interaction was statistically significant. Although we could correctly conclude from one year's data that differences in dormancy between genotypes existed, both the rankings and any estimate of the variation among genotypes would have been in error compared to the two-year mean.

Table 6. Dormancy of _Bothriochloa ischaemum_ genotypes from two harvests.[1]

Genotype	Seed Unit			Caryopsis		
	1958	1959	Mean	1958	1959	Mean
			%			
562	82	34	58	38	27	33
726	83	48	66	31	2	17
3457	76	33	55	57	35	46
5110	36	43	40	13	3	8
6582	78	20	49	49	2	25
6982	54	20	37	13	5	9
6985	73	13	43	21	0	11
7041	34	41	38	9	0	5
7044	55	23	39	27	11	19

[1]Ahring and Harlan 1961. Dormancy calculated by us as germination rough (seed unit) or grain (caryopsis) divided by maximum germination following dormancy breaking procedure (84 to 95%).

Variation within seed lots is a related problem. Even when plants are essentially obligate apomicts, large variability exists (Table 7). Using air column separation, different seed mass classes were easily obtained from seed lots of two lovegrass cultivars. Seed mass values for the subsets ranged from 25 to 35% above and below the mean for the overall seed lot, surely enough to affect performance.

Table 7. Variation within seed lots in 100 caryopsis mass.

	Catalina		Cochise	
	Mean[1]	SD	Mean[1]	SD
		mg/100 seeds		
1[2]	11.0	0.35	6.7	0.35
2	13.7	0.35	8.3	0.17
3	17.6	0.13	9.8	0.31
4	18.8	0.20	11.1	0.10
5	--	--	13.1	0.06
Overall[3]	14.8	0.26	10.5	0.36

[1]Mean of three determinations.
[2]Seed density class obtained by air column separation.
[3]Original seed lot.

We recognize that it may not be possible to fully replicate seed lots, i.e., have a separate lot for each entry replication. It should be possible in most cases to use at least two seed lots per entry when we are trying to characterize seed germination and emergence characteristics of germplasm. The only real alternative may be to grow your own seed under controlled conditions and to present your readers with sufficient data to give them confidence in the quality of that seed. Even then, as illustrated above, there can be serious problems.

SUMMARY AND CONCLUSIONS

Significant genetic variation exists within primary gene pools of warm-season grasses for numerous establishment characteristics. Selection progress has been demonstrated for seed mass, seed dormancy, germination rate, seedling mass, water uptake from seminal roots, and ability to survive drought in controlled environments. Clearly, progress can be made in selecting for all these and other characteristics in most if not all grasses.

What is needed now is to capitalize on several of these characteristics in one selection program. This could be done in several ways. One approach would be to collect all the genetic data, construct a selection index based on all relevant and obtainable characteristics weighted by their value to establishment and then make selections. Selected plants would be allowed to interpollinate (most warm-season grasses are cross-pollinated) followed by additional cycles of selection.

Alternatively, a sequential or tandem approach could be used. Initial selection might be based on caryopsis size followed by selection for speed of germination. Fast germinators could be forced to grow on their seminal roots in a controlled environment to evaluate effectiveness of water uptake. The best survivors of that test might be evaluated for initial adventitious root growth and seedling mass or leaf blade area. Evaluation of growth or survival under moisture and/or heat stress would be added as a final screen. Starting with a large population, the number of individuals screened could be reduced gradually by the various screens to the final population size desired. Selection intensity at the various screens could be varied as appropriate; based on genetic information, an evaluation of the relative importance of that screen, the size of population that could be effectively handled, etc. Seed dormancy might be maintained in the population by heat desiccation or other dormancy breaking procedure prior to selection or dormancy could be selected against. In chaffy-seeded grasses, it might be possible to select against dormancy on a caryopsis basis but allow dormancy to persist on a seed unit basis. This might allow easy and fast germination when needed but retention of seed dormancy in the wild. Many variations of the above would be possible.

Wilson et al.[9] conducted a selection program for several establishment characteristics in blue grama. They selected first for seed mass. Emergence from deep planting, shoot mass, and adventitious root growth were evaluated following intermating. Subsequently, the best survivors were evaluated for seed mass and, on that basis, parents were chosen for intermating and initiation of the next cycle.

Grass breeders working with apomicts will need to take a slightly different approach. Potential apomicts to be used as parents will have to be carefully evaluated. It will be critical to make the best choice to cross to sexual germplasm which may be poorly adapted and could be poor in establishment. Following intermating, the procedure will depend on the inheritance of apomixis. If the breeder is fortunate, some hybrids will be completely sexual, others will be completely apomictic. Apomicts, if superior in establishment and other characteristics, can be considered for release as cultivars. Sexual plants can be used to start a recurrent selection program. Recurrent hybridization to the same or other apomictic genotypes or intermating of sexual plants would be required between cycles of selection. A disadvantage of recurrent hybridization to apomictic sources is the necessity of evaluating each hybrid for mode of reproduction, a time consuming process. After sufficient progress had been made, the breeder would either have to hybridize to an apomictic parent to regain apomixis or use the sexual germplasm directly.

Many variations are possible. What is needed is a commitment to the importance of the work. It means to decide that improving establishment is of sufficient importance to change priorities, whether quickly or slowly, and to get on with what we know needs to be done. Only then will we really learn what can be accomplished genetically to improve stand establishment.

LITERATURE CITED

Abernathy, R. H., and L. N. Wright. 1975. Inflorescence gas exchange and seed weight of blue panicgrass. Crop Sci. 15:383–384.

Abernathy, R. H., L. N. Wright and K. Matsuda. 1977. Association of seedling respiratory metabolism and adenylate energy charge with seed weight of Panicum antidotale Retz. Crop Sci. 17:563–566.

Ahring, R.M., and J. R. Harlan. 1961. Germination characteristics of some accessions of Bothriochloa ischaemum (L.) Keng. Okla. Agric. Exp. Stn. Tech. Bull. T-89.

Anonymous. 1949. Report 3rd West. Grass Breed. Work Plan. Conf. Logan, UT.

Barnett, F. L., and R. L. Vanderlip. 1969. Criteria of field establishment capability in indiangrass Sorghastrum nutans (L.) Nash. Crop Sci. 9:290–293.

Boe, A., and P. O. Johnson. 1987. Deriving a large-seeded switchgrass population using air-column separation of parent seed. Crop Sci. 27:147–148.

Boe, A., and J. Laposky. 1983. Caryopsis weight and seedling vigor in big bluestem (Audropogon gerardii Vet.). Proc. S.D. Acad. Sci. 62:190.

Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. J. Range Manage. 30:276–280.

Cable, D. R. 1965. Damage to mesquite, lehmann lovegrass, and black grama by a hot June fire. J. Range Manage. 18:326–329.

Carren, C. J., A. M. Wilson, R. L. Cuany and G. L. Thor. 1987a. Caryopsis weight and planting depth of blue grama. I. Morphology, emergence and seedling growth. J. Range Manage. 40:(in press)

Carren, C. J., A. M. Wilson, R. L. Cuany and G. L. Thor. 1987b. Caryopsis weight and planting depth of blue grama. II. Emergence in marginal soil moisture. J. Range Manage. 40:(in press)

Cluff, G. J., R. A. Evans and J. A. Young. 1983. Desert saltgrass seed germination and seedbed ecology. J. Range Manage. 36:419–422.

Cooper, C. S., and P. W. MacDonald. 1970. Energetics of early seedling growth in corn (Zea mays L.) Crop Sci. 10:136–139.

Coukos, C. J. 1944. Seed dormancy and germination in some native grasses. J. Am. Soc. Agron. 36:337–345.

Cox, J. R., and G. L. Jordan. 1983. Density and production of seeded range grasses in southeastern Arizona (1970–1982). J. Range Manage. 36:649–652.

Cox, J. R., and M. H. Martin. 1984. Effect of planting depth and soil texture on the emergence of four lovegrasses. J. Range Manage. 37:204–205.

Cox, J. R., M. H. Martin-R, F. A. Ibarra-F and H. L. Morton. 1986. Establishment of range grasses on various seedbeds at creosotebush [Larrea tridentata] sites in Arizona, U.S.A., and Chihuahua, Mexico. J. Range Manage. 39:540–546.

Coyne, P. I., and J. A. Bradford. 1985. Morphology and growth in seedlings of several C4, perennial grasses. J. Range Manage. 38:504–512.

----

[9]Wilson, Cuany, Frazer and Oaks, unpublished.

Dobrenz, A. K., L. N. Wright, A. B. Humphrey, M. A. Massengale and W. R. Kneebone. 1969a. Stomate density and its relationship to water-use efficiency of blue panicgrass (Panicgrass antidotale Retz.). Crop Sci. 9:354-357.

Dobrenz, A. K., L. N. Wright, M. A. Massengale and W. R. Kneebone. 1969b. Water-use efficiency and its association with several characteristics of blue panicgrass (Panicum antidotale Retz.) clones. Crop Sci. 9:213-216.

Eagles, H. A. 1982. Inheritance of emergence time and seedling growth at low temperatures in four lines of maize. Theor. Appl. Genet. 62:81-87.

Frasier, G. W., J. R. Cox and D. A. Woolhiser. 1985. Emergence and survival response of seven grasses for six wet-dry sequences. J. Range Manage. 38:372-377.

Frasier, G. W., J. R. Cox and D. A. Woolhiser. 1987. Wet-dry cycle effects on warm-season grass seedling establishment. J. Range Manage. 40:2-6.

Fulbright, T. E., A. M. Wilson, and E. F. Redente. 1985. Green needlegrass and blue grama seedling growth in controlled environments. J. Range Manage. 38:410-414.

Glewen, K. L., and K. P. Vogel. 1984. Partitioning the genetic variability for seedling growth in sand bluestem into its seed size and seedling vigor components. Crop Sci. 24:137-141.

Hacker, J. B. 1984. Genetic variation in seed dormancy in Digitaria milanjiana in relation to rainfall at the collection site. J. Appl. Ecol. 21:947-959.

Haferkamp, M. R., and G. L. Jordan. 1977. The effect of selected presowing seed treatments on germination of Lehmann lovegrass seeds. J. Range Manage. 30:151-153.

Harlan, J. R. 1950. Establishment and management of grass seedlings. West. Grass Breed. Work Plan. Conf. 4:7-8.

Holt, E. C., J. R. Cain and R. J. Hendler. 1985. Evaluation and management of grasses for dual livestock and gamebird use. J. Range Manage. 38:342-346.

Holzworth, L. K. 1980. Registration of Cochise atherstone lovegrass. Crop Sci. 20:823-824.

Hull, H. M., L. N. Wright and C. A. Bleckmann. 1978. Epicuticular wax ultrastructure among lines of Eragrostis lehmanniana Nees developed for seedling drouth tolerance. Crop Sci. 18:699-704.

Hussey, M. A., and E. C. Holt. 1986. Selection for increased seed weight in kleingrass. Crop Sci. 26:1162-1163.

Johnson, D. A., and K. H. Asay. 1978. A technique for assessing seedling emergence under drought stress. Crop Sci. 18:520-522.

Kneebone, W. R. 1956. Breeding for seedling vigor in sand bluestem (Andropogon hallii Hack.) and other native grasses. Agron. J. 48:37-40.

Kneebone, W. R. 1957. Selection for seedling vigor in native grasses under artificial moisture stress. Agron. Abstr. 49:55.

Kneebone, W. R., and C. L. Cremer. 1955. The relationship of seed size to seedling vigor in some native grass species. Agron. J. 47:472-477.

Major, R. L., and L. N. Wright. 1974. Seed dormancy characteristics of sideoats gramagrass, Bouteloua curtipeudula (Michx.) Torr. Crop Sci. 14:37-40.

Martin, M. H., and J. R. Cox. 1984. Germination profiles of introduced lovegrasses at six constant temperatures. J. Range Manage. 37:507-509.

McConnell, R. L., and C. O. Gardner. 1979. Selection for cold germination in two corn populations. Crop Sci. 19:765-768.

Moore, D. R. J., and P. B. Cavers. 1985. A Comparison of seedling vigor in crop and weed biotypes of proso millet (Panicum miliaceum) Can. J. Bot. 63:1659-1663.

Nason, D. A., R. L. Cuany, and A. M. Wilson. 1987. Recurrent selection in blue grama. I. Seedling water uptake and shoot weight. Crop Sci. 27:(in press)

Nielsen, E. L. 1944. Analysis of variation in Panicum virgatum. J. Agri. Res. 69:327-353.

Pandeya, S. C., and S. J. Pathak. 1978. Germination of some ecotypes of anjou grass (Cenchrus ciliaris) under dry storage and physical stress In D. N. Hyder (ed.) Proc. 1st Internat. Range. Congr. Society for Range Management, Denver, CO.

Pearson, C. J. 1975. Thermal adaptation of Pennisetum seedling development. Aust. J. Plant Physiol. 2:413-424.

Perry, L. J., and L. E. Moser. 1975. Seedling growth of three switchgrass strains. J. Range Manage. 28:391-393.

Potts, H. C., and E. C. Holt. 1967. Parent-offspring relationships in kleingrass, Panicum coloratum L. Crop Sci. 7:145-148.

Rowe, D. E., and D. L. Garwood. 1978. Effects of four maize endosperm mutants on kernel vigor. Crop Sci. 18:709-712.

Silcock, R. G. 1980. Seedling characteristics of tropical pasture species and their implications for ease of establishment. Trop. Grass. 14:174-180.

Smith, R. L. 1979. Seed dormancy in Panicum maximum Jacq. Trop. Agri. 56:233-239.

Takahashii, N. 1978. Adaptive importance of mesocotyl and coleoptile growth in rice under different moisture regimes. Aust. J. Plant Physiol. 5:511-517.

Terrell, E. E., S. R. Hill, J. H. Wiersema and W. E. Rice. 1986. A checklist of names for 3000 vascular plants of economic importance. U.S. Dept. Agric., Agric. Handbook No. 505.

Tischler, C. R., and P. W. Voigt. 1983. Seedling characteristics and rates of seed reserve utilization of wilman lovegrass and kleingrass. Crop Sci. 23:953-955.

Tischler, C. R., and B. A. Young. 1987. Development and characteristics of a kleingrass population with reduced post-harvest seed dormancy. Crop Sci. 27:(in press)

Turner, F. T., C. C. Chen and C. N. Bollich. 1982. Coleoptile and mesocotyl lengths in semidwarf rice seedlings. Crop Sci. 22:43-46.

Voigt, P. W., and J. E. Adams. 1977. Root growth of warm-season grass seedlings. Grass Breed. Work Plan. Conf. 24:8.

Voigt, P. W., and H. W. Brown. 1969. Phenotypic recurrent selection for seedling vigor in side-oats grama, Bouteloua curtipendula (Michx.) Torr. Crop Sci. 9:664-666.

Wann, E. V. 1980. Seed vigor and respiration of maize kernels with different endosperm genotypes. J. Am. Soc. Hort. Sci. 105:31-34.

Watt, L. A. 1974. The effect of water potential on the germination behavior of severl warm season grass species, with special reference to cracking black claysoils. J. Soil Conserv. N.S.W. 30:28-41.

Weaver, L. C., and G. L. Jordan. 1985. Effects of selected seed treatment on germination rates of five range plants. J. Range Manage. 38:415-418.

Wilson, A. M. 1981. Air and soil temperature effects on elongation of adventitious roots in blue grama seedlings. Agron. J. 73:693-697.

Wilson, A. M., R. L. Cuany, J. G. Fraser and W. R. Oaks. 1981. Relationship among components of seed yield in blue grama. Agron. J. 73:1058-1065.

Wilson, A. M., and J. A. Sarles. 1978. Quantification of growth drought tolerance and avoidance of blue grama seedlings. Agron. J. 70:231-237.

Wright, L. N. 1971a. Germplasm potentials among blue panicgrass (Panicum antidotale Retz.) sample populations. Crop Sci. 11:751-753.

Wright, L. N. 1971b. Registration of Catalina weeping lovegrass. Crop Sci. 11:939.

Wright, L. N. 1971c. Drought influence on germination and seedling emergence In K. L. Larson and J. D. Eastin (eds.) Drought Injury and Resistance in Crops, Special Pub. No. 2, Crop Science Society of America, Madison, WI.

Wright, L. N. 1975. Improving range grass for germination and seedling establishment under stress environments, pp. 3-22 In R. S. Campbell and C. H. Herbel (eds.) Improving Range Plants, Range Symp. Ser. No. 1. Society for Range Management, Denver, CO.

Wright, L. N. 1976. Recurrent selection for shifting gene frequency of seed weight in Panicum antidotale Retz. Crop Sci. 16:647-649.

Wright, L. N. 1977. Germination and growth response of seed weight genotypes of Panicum antidotale Retz. Crop Sci. 17:176-178.

Wright, L. N. 1978a. Recurrent selection for changing gene frequency of germination rate in blue panicgrass. Crop Sci. 18:789-791.

Wright, L. N. 1978b. Registration of Kuivato and Puhuima lehmann lovegrass. Crop Sci. 18:912-913.

Wright, L. N. 1980. Germination rate and growth characteristics of blue panicgrass. Cro Sci. 20:42-44.

Wright, L. N., and S. E. Brauen. 1971. Artificial selection for seedling drouth tolerance and association of plant characteristics of lehmann lovegrass. Crop Sci. 11:324-326.

Wright, L. N., and A. K. Dobrenz. 1970. Efficiency of water use and seedling drouth tolerance of boer lovegrass, Eragrostis curuula Nees. Crop Sci. 10:1-2.

Wright, L. N., and A. K. Dobrenz. 1973. Efficiency of water use and associated characteristics of lehmann lovegrass. J. Range Manage. 26:210-212.

Wright, L. N., and G. L. Jordan. 1970. Artificial selection for seedling drouth tolerance in boer lovegrass (Eragrostis curuula Nees). Crop Sci. 10:99-102.

ANNUAL LEGUME GERMPLASM EXPLORATION AND TESTING
TO IMPROVE RANGE, PASTURE AND SOILS IN THE
WINTER-RAINFALL CALIFORNIA CLIMATE

W. L. Graves[1], B. L. Kay, M. B. Jones, W. M.
Jarrell, A. Murphy, M. George, C. Adams, J.
Burton, J. Young, R. Clary, R. Slayback, V.
Wegrzyn, D. C. Mendoza, and J. Chavez[2].

ABSTRACT

Six years of plant exploration and testing of
subclover (*Trifolium subterraneum* L.), and their
associated nitrogen fixing *Rhizobium* bacteria
has identified encouraging candidates for
California and Baja California in Mexico.
Selection and adaptation experiments are dis-
cussed. Plant establishment and management of
promising subclover strains are highlighted.

INTRODUCTION

Range and pasture studies in the foothill,
central and southern coastal areas of California
show that forage production is low and quality
poor during an important part of the year.
Important contributing factors are the soils and
annual vegetation types in these zones. Soils
are usually highly deficient in nitrogen.
Productivity and quality of the naturalized
annual vegetation is low. Animal performance is
poor without costly external inputs of
fertility.

Production of nitrogen fertilizer, a key element
for obtaining high production on range and
pasture areas, requires high energy and fossil
fuel inputs for its commercial production.
Since the energy crisis of 1973, nitrogen
fertilizer has become a questionable economic
value for forage production.

The productive naturalized annual legume, bur
clover (*Medicago polymorpha* var. *nigra* L.) has
and is being decimated in some California ranges
by the alfalfa weevils (*Hypera postica* and *H.
brunneipennis*). The introduction of other
Mediterranean adapted annual legumes capable of
biologically vixing significant amounts of

nitrogen is promising, not only in California,
but in Australia, North Africa, the Middle East,
Baja California, and the SE United States
(Murphy et al., 1973). Our successes in
northern California with the early introduc-
tions of annual legumes, such as subclover
(*Trifolium subterraneum* L.) from Australia,
were highly dependent on adequate well distri-
buted moisture. Rainfall amounts and distribu-
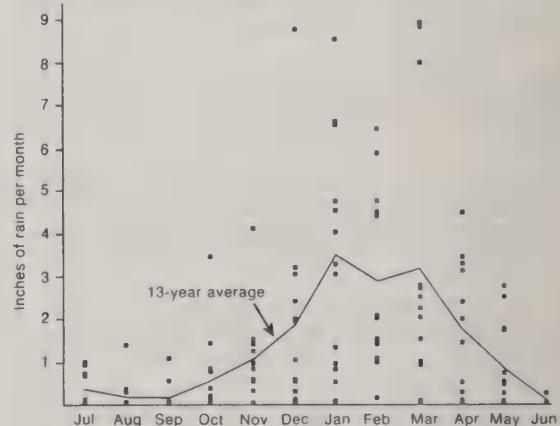tion are less dependable in southern California
(fig. 1).
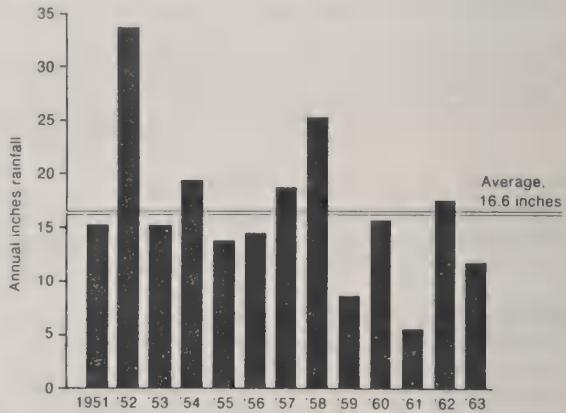
Figure 1. Yearly and monthly 13-year rainfall
patterns for a typical southern
California range site (13-year
summary).

[1]Farm Advisor, UCCE, Bldg. 4, 5555 Overland
Ave., San Diego, CA 92123.

[2]Specialist, UCD; Agronomist, UCD; Professor,
UCR; Superintendent (Retired), Hopland Field
Station; Specialist, UCCE-UCD; Statistician,
UCCE-UCR; Microbiologist, Retired; Range
Scientist, USDA-ARS; PM Manager, USDA-SCS; PM
Specialist, USDA-SCS-Davis; Professor, UCR;
Professor, UBC-Mexicali, Range Specialist,
INJA, Ensenada, Respectively.

The study by Williams and Elliot (1960) of seed
coat impermeability of three annual legume
species pointed out the importance of
hardseededness as an adaptation and a survival
mechanism in a sometimes harsh and highly
variable rainfall pattern of the California
climate. In the late 1960's and since, this
factor has come to be recognized and
incorporated into the subclover plant
exploration selection and breeding programs of
the range and pasture scientists of Australia,

(Francis et al., 1970; Gladstones 1975; Francis and Gladstones, 1983). Although both rose clover (*Trifolium hirtum* L.) and annual medics (*Medicago* sp.) have long been recognized as species with a high degree of hardseededness, the subclover germplasm is recognized as having the most potential in California if a suitable hardseeded strain can be developed (Love and Sumner, 1952; Williams and Elliott, 1960; Trumble 1939). Thus a plant introduction program was established to improve our subclover hardseededness resources. During 1979 to 1981 a plant and *Rhizobium* exploration program was begun in Tunisia, and it was expanded to Morocco in 1983 (Rumbaugh and Graves, 1984). Plant material exchanges with our Australian colleagues allowed us to augment our germplasm bank. With these resources we began our search for high hardseeded subclovers adapted to our California ranges and pastures.

EXPERIMENTAL PROCEDURE AND BACKGROUND

Taking advantage of our Tunisian plant and *Rhizobium* collection and the materials from our Australian exchanges, we began the first stage nursery seed increase and preliminary screening in the late fall, 1981. Using the 1981 and 1982 nursery performances and the strain information developed by Gladstones (1967) on the Australian naturalized strains, we screened the germplasm based on hardseededness, low to moderate oestrogen, good winter vigor and early to medium maturity. The test location was the Hopland Field Station located at 240 m elevation with mean rainfall of 934 mm. During the first two years of the trial the rainfall was above average, and the third year was below.

We selected two Tunisian strains (Trsu-405 and Trsu-400), six Moroccan strains (WA65320, WA65321-A, WA65324-J, SA65324-L, WA65331-D, and WA65332-E), one strain from Italy (WA47275), one from Turkey (SA15077), five naturalized Australian ecotypes (Baulkamaugh, Bellevue, Collie B, Grayland and Mulwala) and two Australian standard cultivars (Woogenellup and Enfield). The selections were planted at the Hopland Field Station on October 14, 1983 on a Yorkville acid clay soil (Pachic Argixerolls). All seeds were "Pelinoc" pellet inoculated with a specific sub/rose clover inoculant and seeded in three rows 30 cm apart at the rate of 112 kg/ha into plots 1.5 x 3 m and replicated in three blocks. Phosphate and sulfur were added at adequate rates. During the establishment year, the plots were mowed to control weed contamination and grass competition. On April 30, 1984 the plots were sampled for above ground seasonal plant production by clipping 30 cm square quadrats to ground level. During the 1984/85 growing season the plots were mowed to simulate grazing. During each of the first two summers, sheep were used to remove the dry plant residue. At the beginning of the October 1985 rainy season, the seed heads from two of the reps were sampled in 30 cm quadrats to a soil depth of 1 cm. The seed pods were subsequently removed from the soil, and the seeds were carefully

removed from the pods so as to not scarify any of the seeds. The seeds were then subjected to a replicated germination test to assess germination and hardseed percentages. In March of 1986, before flower initiation, the plants on the plots were killed with a systemic herbicide to prevent seed production and simulate the effect of an erratic rainfall pattern. Following an early rain in late September 1986 the plots were again rated for stand emergence using a 0 to 10 rating system (0=no plants, 10=total plot emergence).

RESULTS AND DISCUSSION

Subclover establishment, beginning third year hardseededness and fourth year regeneration results are summarized for the 18 accessions in Table 1. There were no significant differences between strains in forage production. Because all strains flowered and set mature seeds, we assumed that all completed the establishment season with an equal chance for regeneration and long term adaptation.

By the beginning of the third growing season, the hardseededness results show a great diversity among the 18 test strains. Results are consistent with the Australian experience with their test strains and the two commercial varieties, Woogenellup and Enfield (Francis et al., 1970; Francis and Gladstones, 1983; Collins et al., 1984). Some contamination between plots has been observed. We were able to detect this factor because of the inclusion of WA 65321-A, a cream colored strain, while all other strains were dark seeded. Some dark seeds were observed in this strain's harvest. Two other strains (WA 47275 and Woogenellup) appear to have contamination due to the large differences in the hardseededness reading. WA 47275 is probably a lot harder than the mean figure, 53 percent, indicates and may be one of the more promising hardseeded species. Woogenellup, on the other hand, is probably softer than the low mean figure, 20 percent, would indicate, since the low reading was only two percent hardseededness. Under Australian conditions Woogenellup is considered to be a relatively soft seeded cultivar. The naturalized Australian ecotypes, Bellevue, Tooday B, Mulwala and Collie B., demonstrated hardseedness at the Hopland Field Station is quite similar to those values obtained by Francis et al. (1970) in Western Australia, as did the Moroccan strain, WA 65321-A. (Francis and Gladstones, 1983).

The stand regeneration evaluation made at the beginning at the fourth season lends more validity to the hardseededness factor as being important to stand regeneration following stand failures. Four of the experimental hardseeded strains demonstrated a significantly higher stand regeneration than the best commercial cultivar, Woogenellup. As for the cultivar Enfield, twelve of the experimental hardseeded strains demonstrated a significantly higher stand generation than this recently developed Australian cultivar. Since the Enfield cultivar is being promoted to replace the older

Table 1. Evaluation of subclover strains for first year establishment,
beginning third year hardseededness, and fourth year regen-
eration at the Hopland Field Station, CA.

	YEAR		
Strain/Cultivar	First Year Establishment 4/30/84	10/85	10/86
	Dry Matter Yield per Plot 0.09 sq. m[1]	Percent Hardseed[2]	Clover Stand Regeneration (0-10)[3]
Tooday B	75	82	9
WA 65324-J	91	80	4
Baulkamaugh	80	74	6
Grayland	92	73	9
SA 65324-L	94	67	6
WA 65321-A	85	66	5
WA 65331-D	77	63	6
Trsu-400	106	62	4
WA 47275	82	53	4
WA 65332-E	81	53	3
WA 65320	94	53	7
SA15077	85	52	8
Trsu-405	76	52	7
Bellevue	66	51	9
Collie B	74	49	7
Mulwala	84	33	9
Woogenellup	101	20	5
Enfield	96	8	1
Mean	85		6
LSD (0.05)	NS		3

[1] Means from 3 reps
[2] Means from 2 reps
[3] Means from 3 reps, (0=no emergence, 10=total plot emergence)

Woogenellup cultivar, we would express caution at this recommendation.

The correlation of the October 1985 hardseeded percentage and the October 1986 stand regeneration is significant at the 5 percent level.

SUMMARY AND CONCLUSION

Several factors are considered important in the successful establishment and persistence of subclover stands in the cool-season rainfall-dry summer climate of California. Namely, the choosing of an adapted cultivar, use of phosphate and sulfur, pellet inoculation with specific *Rhizobium* strains (Jones et al., 1978), seeding just prior to the rainy season into a proper seedbed, adequate and timely rainfall and livestock management during the establishment and subsequent life of the clover stand.

Grazing during the growing season is important to enhance its establishment and persistence. Proper grazing management can help to control undesirable weeds, optimize seed production, maintain a proper grass-legume balance and increase nitrogen recycling.

Although numerous Australian cultivar introductions have occurred over the last several decades most have been soft seeded cultivars and they have had limited success outside of the northern California high rainfall zones. The finding and testing of hardseeded subclover strains is believed to be the first step in extending this highly versatile range and pasture germplasm to other parts of California with lower yearly rainfall totals and a high degree of variability in both yearly rainfall and its seasonal distribution.

The results obtained in this study with a limited number of hardseeded strains (16) at the Hopland Field Station in Mendocino Co., California, indicate that hardseeded strains still exist in their native habitat. These strains maintain their hardseededness under California conditions, and they offer a potential for adaptation under a number of varied California conditions. The significant relationship between hardseededness and stand regeneration following stand failure from induced drought conditions would seem to justify the continued evaluation of subclover germplasm

for the hardseededness factor with the aim of improving pasture and range animal productivity without using large inputs of high energy non-renewable fossil fuel resources.

Disclaimer: To simplify information, trade names of products have been used. No endorsement of named products is intended nor is any criticism implied of similar products which are not mentioned.

LITERATURE CITED

Collins, W. J., C. M. Francis and B. J Quinlivan. 1984. Registered cultivars of Subterranean clover - their origin, identification, and potential use in Western Australia. Western Australian Dept. of Agriculture Bulletin 4083, 28 p.

Francis, C. M., J. S. Gladstones, and W. R. Stern. 1970. Selection of new Subterranean clover cultivars in southwestern Australia. Proc. of the XI International Grassland Congress, Surfers Paradise, p. 214-218.

Francis, C. M., and J. S. Gladstones. 1983. Exploitation of the genetic resource through breeding: *Trifolium subterraneum*. p. 251-260 in J. G. Melvor and R. A. Bray (eds.) Genetic Resources of Forage Plants, CSIRO, East Melbourne.

Gladstones, J. S. 1967. Naturalized subterranean clover strains in Western Australia: A preliminary agronomic examination. Aust. J. of Agric. Res. 18:713-731.

Gladstones, J. S. 1975. Legumes and Australian agriculture. J. of Aust. Inst. of Agric. Res. 41:227-240.

Jones, M. B., J. C. Burton and C. E. Vaughn. 1978. Role of inoculation in establishing subclover on California annual grasslands. Agronomy J. 70:1081-1085.

Love, R. M., and D. C. Sumner. 1952. Rose clover - a new winter legume. U. of Calif. Ag. Exp. Sta. Circ. 407, 12 p.

Murphy, A. H., M. B. Jones, J. W. Clawson, and J. E. Street. 1973. Management of clovers on California annual grasslands. U. of Calif. Ag. Exp. Sta. Circ. 564, 19. p.

Rumbaugh, M. D. and W. L. Graves. 1984. Foreign travel report: Collecting germplasm in Morocco. Abstracts Western Alfalfa Improvement Conf., 20-21 Sept., 1983, Lethbridge, p. 92-97/

Trumble, H. C. 1939. Barrel medic (*Medicago tribuloides*, Desr.) as a pasture legume. J. Dept. Agric. South Aust. 42:953-958.

Williams, W. A. and J. R. Elliot. 1960. Ecological significance of seed coat impermeability to moisture in crimson, subterranean and rose clovers in a Mediterranean climate. Ecology 41:785-790.

SOIL MOISTURE AVAILABILITY EFFECTS ON SEED GERMINATION AND GERMINATED SEED SURVIVAL OF SELECTED WARM SEASON GRASSES

Gary W. Frasier[1]

ABSTRACT

Germination rates and germinated seed survival under limited soil moisture conditions of five warm-season grass species were evaluated in laboratory growth chambers. Techniques were developed to relate seed germination characteristics at reduced soil water potentials to field soil moisture tension conditions for estimating potential rates and percentages of seed germination.

INTRODUCTION

Soil moisture availability is among the key factors affecting seed germination and seedling survival under rainfed conditions. With dry soil conditions, seeds will not initiate germination. During periods of wet soil, the seeds germinate and produce viable seedlings which develop into mature plants. If the initial wet period during germination or seedling growth is followed by an extended dry period, the germinated seed or seedling may die. Understanding the germination and survival characteristics of germinated seeds and seedlings, as affected by available soil moisture, offers the possibility of incorporating the probabilistic aspects of precipitation and soil water relations into a description of the seedling environment necessary for plant establishment.

To accomplish this task, information is needed on the critical length of the 'wet' period required for seed germination in soil. Information is needed on the quantity and/or tension of available soil water which constitutes a 'wet' condition from the perspective of the seed. And finally, information is needed on the effect of the relative length of the first dry period following planting on germinated seed survival.

Laboratory growth chamber studies were conducted to: (1) evaluate the survival characteristics of germinated seeds during extended periods of high moisture tensions, (2) evaluate the rate of seed germination at various soil moisture tensions, and (3) develop a technique for relating seed germination rates to field seedbed soil moisture conditions during drying. For the studies a germinated seed was defined as the stage of growth when the seed had a visible radicle but before a shoot had emerged.

BACKGROUND

Frasier et al. (1985), found that the seedling survival probabilities of seven warm-season grasses exposed to the first wet-dry watering sequence following seeding were a function of: (1) the number of seedlings produced in the first wet period which developed sufficient vigor to survive the subsequent dry period; (2) the number of ungerminated but viable seeds which remained after the first wet-dry watering sequence; and (3) the relative lengths of the wet and dry periods. The study did not provide information on the relative effects of the wet-dry watering sequences on seed germination or what constituted a 'wet' or 'dry' condition from a seed/seedling perspective.

Determining the effect of the quantity of available water on seed germination in a soil medium is difficult because the soil cover prevents direct observation of the germination process. One relatively common technique for evaluating the effect of water availability on germination is to place the seeds in salt or polyethylene glycol (PEG) solutions of various concentrations (Kaufmann and Ross 1970). These approaches are straight forward, suitable for laboratory controlled environments, and provide a rapid assessment of the relative differences in germination rates and total seed germination potential. There is a large volume of data in the literature on seed germination of many plant species in salt or PEG solutions. Unfortunately it is difficult to directly compare the results of various studies. It is usually necessary to develop some type of analytic relation for interpolating or extrapolating the results for comparison purposes.

There is also some concern that the results derived in solution studies are not representative of field results that might occur at the same matric water potentials. Kaufmann and Ross (1970), reported that PEG solutions do not represent many soil situations because the germination rate in solutions was much more rapid than that observed in the field. Earlier, Collis-George and Sands (1962), in studies utilizing different solutes at the same osmotic potential, found that osmotic and matric potentials were not interchangeable in their qualitative influence on seed germination. Sedgley (1963), concluded that the matric soil-water potential was not controlling seed germination. Rather the area of water contact with the seed was the more important factor. This theory was partially substantiated by Collis-George and Hector (1966), who found that there was an effect of the area of water contact at the higher matric potentials. Sharma (1973), found that total germination in PEG solutions and soils were similar if there was good seed-soil contact, water movement in the soil was non-limiting, and there was no undesirable microbial growth.

The water-seed contact area becomes an important factor with small seeds which approach the size of the soil particles. Hunter and Erickson (1952), reported that soil moisture tension but not soil texture, affected the germination of soybeans (_Glycine max_), corn (_Zea mays_), rice (_Oryza_ spp.), and sugar beets (_Beta vulgaris_ L.). With smaller sized seeds of Russian thistle, (_Salsola kali_ var. _tenuifolia_ Tausch), germination in a clay soil and

[1]Research Hydraulic Engineer, USDA-ARS, Aridland Watershed Management Research Unit, 2000 East Allen Road, Tucson, Arizona 85719.

PEG solutions were similar. Germination of Russian thistle seeds in coarser textured loam and sandy soils was greatly reduced at matric potentials less than -2 bars (Young and Evans 1972). Similar results were obtained with cultivars of subclover (Trifolium subterraneum L.) (Young et al. 1970).

Once germination has occurred, the germinated seed and seedling are in a growth stage where adequate soil water can become a critical factor for continued growth and survival. Watt (1978), reported a complete loss of seed viability when germinated seeds of Queensland blue grass (Dicanthium sericeum L.) were placed in air-dry soil for 9 days then rewetted for 14 days. In another study, the survival of partially germinated seeds of bambatsi panic (Panicum coloratum L.) native millet (Panicum decompositium R. Br.), wallaby grass (Danthonia lavevis Vickery), windmill grass (Chloris truncata R.Br.), and purple pigeon grass (Setaria porphyrantha Stapf) was less than 50%. A germinated seed was defined as between "...when the colorhiza and/or coleoptile emerged from the caryopsis.", and "...when the emerging radicle and/or shoot broke through the colorhiza or coleoptile." (Watt 1982). Hassanyar and Wilson (1978), found that the differences in the ability of crested wheatgrass (Agropyron desertorium [Fisch.ex Link] Schult.) and Russian wildrye (Elymus junceus Fischer) to survive a dry period following germination but prior to seedling development was correlated with the ability of the species to develop seminal lateral roots. Fulbright et al. (1984), found that dehydration of germinating seeds of green needlegrass (Stipa viridula Trin.) significantly reduced subsequent seedling emergence.

There are very little data concerning the actual soil-water tensions which exist in the shallow seedbed zone of many rangeland sites. Wilson et al. (1970), reported that water potentials in the surface soil decreased from -4 bars to -300 bars in a 2-day period. Soil water content changes equivalent to water potential changes of -2 bars to over -15 bars occurred in the surface 0.5 cm of soil with a single day of drying (Nakayama et al. 1973, Jackson 1973, private correspondence with R. D. Jackson).

MATERIALS AND METHODS

Germinated Seed Survival

The study was to evaluate the length of time that newly germinated seeds would remain viable on dry filter paper in a 95 to 100% R.H. incubator. This information is needed to determine the susceptability of germinated seeds to severe dessication following initial germination. The plant species used in the studies were; 'Premier' sideoats grama (Bouteloua curtipendula (Michx.) Torr.), 'A-68' Lehmann lovegrass (Eragrostis lehmanniana Nees), 'Catalina' lovegrass (E. curvula var. conferta (Schrad.) Nees), 'Cochise' lovegrass (E. lehmanniana Nees X E. trichophora Coss and Dur.), and 'SDT' blue panicgrass (Panicum antidotal Retz).

Seeds were germinated between two disks of Whatman No. 3 filter paper in 8.5-cm diameter x 1.5-cm deep petri dishes. The filter paper was saturated with deionized distilled water, covered with a lid and placed in an 29.4 C incubator for sufficient time to germinate most seeds. The time for initial seed germination varied from 15 to 68 hours (Table 1). The start time for the initial germination phase was staggered so that the seeds of all species would be at approximately the same stage of germination for the dessication phase of the study.

Table 1. Seed germination time.

Species	Time for initial germination
	(hrs)
Sideoats grama	15-16
Catalina lovegrass	50-52
Cochise lovegrass	66-68
Lehmann lovegrass	50-52
Blue panicgrass	50-52

Ten germinated seeds per species with a visible radical less than 3 mm long were individually selected and placed between two layers of dry Whatman No. 3 filter paper in petri dishes. The petri dishes were randomly placed in a constant temperature incubator for the various dry period intervals. Following the dry period, the filter paper was wetted with distilled water and the petri dishes returned to the incubator (at the prescribed temperature) for 7 days at which time the number of surviving germinated seeds were counted.

The experimental design included six dry period intervals, five species, three temperatures, and three replications in time. Each replication consisted of the pooled count of six petri dishes. The dry period intervals were; 0, 1, 3, 5, 7, and 10 days. The incubator temperatures were 22, 29 and 35°C. Replication means of the surviving seed counts were subjected to analysis of variance to determine if differences among species, temperature and lengths of dry periods were significant.

Seed Germination at Reduced Water Potential

The objective of this study was to evaluate the rate of seed germination in selected soils at reduced water potentials. Three soils were used: a Vekol silty clay loam (thermic, Typic Haplargid) from the east side of Avra Valley, 25 km west of Tucson, AZ; a Sonoita silty clay loam (thermic, Typic Haplargid) from near Three Points, AZ, 50 km west of Tucson, AZ; and a Comaro sandy loam (mixed, thermic, Typic, Torrifluvent) from the Santa Rita Experimental Range 60 km south of Tucson, AZ. (Soil description provided by Jack Stroehlein, University of Arizona, personal communication) The Avra Valley and Three Point soils were abandoned irrigated farmland areas.

The Santa Rita soil was from a semiarid grassland pasture. A composite soil sample representing the top 4 cm was collected at each site. Based upon the particle size distribution (hydrometer), the composite samples from the Three Points and Santa Rita areas were both classified as a sandy loam. The soils are dissimilar in their proportions of sand and silt. The textural analysis of the Avra Valley sample was a sandy clay loam (Table 2).

Table 2. Particles size distribution of the Avra Valley, Three Points and Santa Rita soils.

Soil	Sand	Silt	Clay	Soil texture classification
	(%)	(%)	(%)	
Avra Valley	43.3	34.1	22.6	sandy clay loam
Three Points	53.3	45.1	1.6	sandy loam
Santa Rita	69.4	22.2	8.4	sandy loam

Soils were sieved through a 4 mm screen. Approximately 250 g were placed on the surface of a prewetted ceramic plate in a pressure chamber. The soil was saturated with distilled water and pressures of 0.3, 1.0, or 7.0 bars were applied to the chamber for 24 hours. Three pressure chambers were used simultaneously, one for each pressure. Each pressure chamber held three pressure plates, one for each soil. After 24 hours approximately 35 g of soil from the pressure plates were placed in 6.0 cm diameter X 4.5 cm deep metal soil cans and lightly compacted with a rubber stopper. Ten seeds were placed on the soil surface and covered with a 1-2 mm layer of lightly compacted soil. The cans were covered with a lid and randomly placed in a 26.7°C constant temperature incubator. Each can was inspected daily for 14 days and the number of germinated seeds counted. A seed with any visible sign of a radicle was considered as germinated and was removed after counting. Each replication consisted of the pooled count from three cans (30 seeds). Two, 50-g, soil samples were collected from each soil and at each tension for gravimetric determination of the soil water content.

The rate of seed germination at zero (0) water stress was determined in petri dishes filled with 50 g of soil saturated with distilled water. Thirty seeds were placed uncovered on the soil surface, the dish covered, and placed in a 26.7°C incubator (one dish per species). The number of germinated seeds were counted daily for 12 days.

An estimate of the relative rate of germination without soil was determined by placing 30 seeds between two disks of Whatman No. 3 filter paper wetted with distilled water in covered petri dishes. The dishes were placed in a 26.7°C incubator for nine days. The number of germinated seeds were counted daily.

The experimental design consisted of five grass species, three soils, four water tensions (0, -0.3, -1.0, and -7.0 bars) and three replications. The accumulated daily plant count for each replication for each species, soil, and water tension was fitted by least squares techniques to the equation;

$$y = A + B \ln (x) \tag{1}$$

where,

y = the accumulative plant count, and
x = time in days.

Replication means of the linear regression coefficient (B) were subjected to analysis of variance to determine the differences in the best fit lines representing the responses in seed germination among species, soils and water potentials. When "F" values were significant, (P < 0.05), Duncan's new multiple range test was used to separate means (Hruschka 1973).

RESULTS AND DISCUSSION

Germinated Seed Survival

Analysis of variance of the results showed no differences among temperatures on the survival of the germinated seeds on the dry filter paper. There was a significant interaction between species and number of dry days (P < 0.05).

The results show that germinated seeds of sideoats grama were significantly more tolerant to severe drought periods of up to three days than the other four species evaluated. The mean seedling survival percentages with time across all temperatures for the five species are presented in figure 1. The differences in germinated seed survival required for significance on any day is 26.2% (P < 0.05). While not statistically significant, the results indicated that approximately 15% of the germinated sideoats grama seeds survived on dry filter paper for periods of up to 10 days.
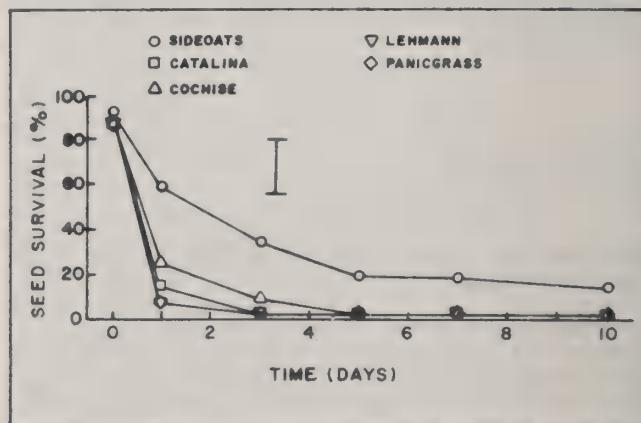

Figure 1. Survival of germinated seeds of five warm-season grasses on dry filter paper. The vertical bar represents the differences, (LSD), required for significance (P<0.05).

These results implied that germinated sideoats grama seeds are more tolerant of a short-term drought than the three lovegrasses and the blue panicgrass. This evaluation procedure was originally considered a "harsh" test with the water tensions on the filter paper greater than the "wilting point" of -15 bars. This may not be that unrealistic. Evans and Young (1972) showed a rapid drying of the surface soil in shallow seedbeds. Wilson et al. (1970) showed soil moisture tensions in excess of -15 bars after a few days of drying. The test may be a good evaluation of drought resistance of germinated seeds.

Seed Germination at Reduced Soil Water Potential

The soil water contents at the three water potential levels at the time of seeding were highest with the sandy clay loam and lowest with the sandy loam from Santa Rita (Table 3).

Table 3. Soil water contents (mean and standard deviations, [SD]), by weight of three soils at three moisture tensions.

Soil	Soil Moisture Tension-bars					
	0.3		1.0		7.0	
	Mean	SD	Mean	SD	Mean	SD
	(%)	(%)	(%)	(%)	(%)	(%)
Avra Valley (sandy clay loam)	13.47	1.00	11.05	0.27	10.06	0.16
Three Point (sandy loam)	10.86	0.43	9.08	0.57	7.24	0.97
Santa Rita (sandy loam)	5.33	0.57	4.01	0.11	3.47	0.28

Analysis of variance of the coefficient (B) of the regression equation for the germination-time responses for the four water tension levels showed no differences among soil type ($P < 0.05$). The absence of any differences among soils with different water holding capacities shows that the germination process was affected by soil-water tension and not soil-water content.

There were differences among species and moisture tension levels and an interaction between species and soil moisture tension ($P < 0.05$). The values of the coefficients (A) and (B) of the regression equation of the pooled values across soils for the four soil-moisture levels and the filter paper based on 30 seeds are presented in Table 4.

The regression coefficient (B) for the germination rates were similar between the filter paper and the zero water stress on soils. While not always statistically significant, there was a general decrease in germination rate and total germination percentages with increasing soil moisture tensions with all species.

The final germination percentage of sideoats grama was considerably lower than expected because of some loss of seed viability, the cause of which is unknown. It is not known if this affected the rate of seed germination as represented by the regression coefficients (A) and (B). The coefficient (B) for the sideoats grama across the four soil-moisture levels did not differ significantly ($P < 0.05$) (Table 4).

No differences in the germination-time response curves (coefficient B) were found with the blue panicgrass until the soil-moisture tension was increased from -1 bar to -7 bars (fig. 2). Similar differences in the coefficient (B) occurred with the three lovegrasses, but at soil-moisture tensions changes of 0.0 to- 0.3 bars as illustrated with Lehmann lovegrass (fig. 3). These results show the potential sensitivity that some species have to soil-water tensions. Even with the soil at "field capacity" (-0.3 bars), the rate of seed germination and total germination percentages may be reduced by 50% or more compared to germination at zero (0) water stress in soil or on filter paper.
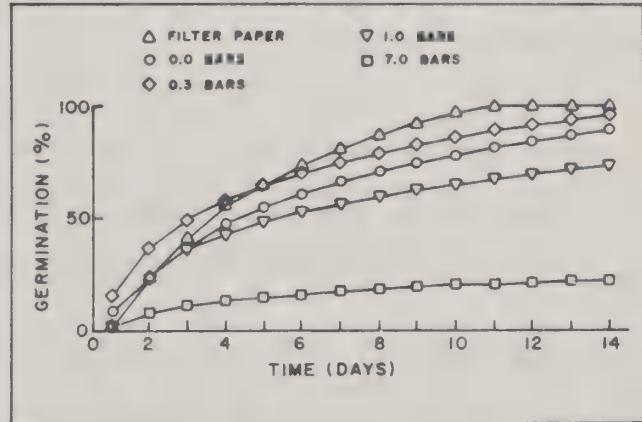

Figure 2. Germination of blue panicgrass on filter paper and in soil at 4 moisture tension levels.
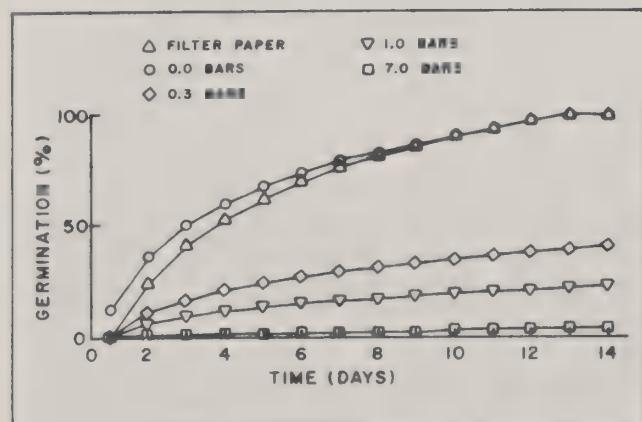

Figure 3. Germination of Lehmann lovegrass on filter paper and in soil at 4 moisture tension levels.

Table 4. Means of the coefficients (A) and (B) of the regression curves[1] representing the germination with time of five grass species on filter paper and four soil water potentials. Data are the pooled results from the three soils.
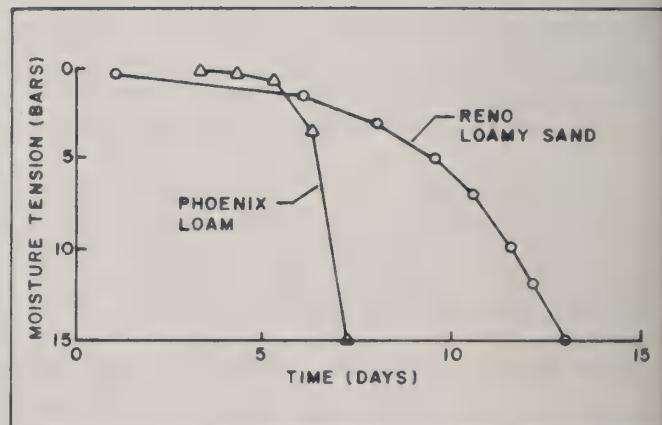
| | | | Soil Moisture Tension-bars | | | |
Species	Coef.	Filter Paper	0.0	0.3	1.0	7.0
Lehmann lovegrass	A	-0.948	3.706	0.497	0.280	-0.009
	B	12.127	10.280 a[2]	4.436 b	2.470 b	0.427
	r^2	.968	.878	.874	.782	.799
Catalina lovegrass	A	-2.312	0.267	0.028	0.130	-0.053
	B	12.178	9.270 a	5.667 ab	2.046 bc	0.591
	r^2	.964	.876	.935	.820	.797
Cochise lovegrass	A	-3.286	-1.338	-0.747	-0.206	-0.077
	B	9.354	8.636 a	3.385 b	0.860 b	0.241
	r^2	.938	.862	.874	.805	.664
Sideoats grama	A	1.412	2.318	1.735	1.573	0.434
	B	3.442	2.729 a	2.775 a	2.609 a	1.024
	r^2	.930	.713	.757	.729	.756
Blue panicgrass	A	-2.597	0.002	4.658	2.571	1.019
	B	13.806	10.236 a	9.189 a	7.413 a	2.155
	r^2	.957	.915	.760	.815	.796

[1]Y = A + B Ln (X), where (Y) is the plant count resulting from 30 seeds on day (X). Analysis of variance was run only on the cofficient (B) for the four soil moisture tensions.

[2]Values in a row with different letters are significantly different at P<0.05.

APPLICATION OF RESULTS

Field data showing changes in soil water tensions in shallow seedbeds (0-1 cm) during drying is limited. Evans and Young (1972) presented data of soil moisture tensions during drying from fields in February in the top 1.5 cm of a loamy sand soil near Reno, Nevada. Similar data for the top 0.5 cm of a loam soil drying in March near Phoenix, Arizona was reported by Jackson (1973) and Nakayama et al. (1973)[1] (fig.4).

---

[1]Data were reported as volumetric water contents which were converted to soil moisture tensions by the following equation provided by R.D. Jackson, U.S. Water Conservation Laboratory, USDA-ARS, Phoenix, Arizona.

$$\psi = \exp [14.86 + 25.65\theta - 1773.7\theta^2 + 19163.2\theta^3 - 97687.7\theta^4 + 236565\theta^5 - 218317\theta^6]$$

where ψ = soil moisture tension in bars, and
θ = volumetric water content

Figure 4. Soil moisture changes with time during drying of the seedbed zone of a loamy sand soil near Reno, NV in February and a loam soil near Phoenix, AZ in March. From Evans and Young (1972), Jackson (1973) and Nakayama et al. (1973).

Least squares techniques were used to fit the soil water tension data to the equation

$$y = a\ e^{bx} \qquad (2)$$

where y = soil water tension in bars, and
x = time in days.

Table 5 presents the regression coefficients (a) and (b) for equation (2) for the two soils. Other soils at different times of the year and climatic conditions may have different soil moisture tension responses to drying.

Table 5. Coefficients (a) and (b) of the regression curve[1] representing the soil moisture tensions with time during drying of two soils.

Soil	Coefficient	
	a	b
Loamy sand- Reno	0.183	0.343
Loam- Phoenix	0.00029	1.495

[1]Equation (2)

Solving equation (2) for (x),

$$x = (1/b)\ \ln\ (y/a), \qquad (3)$$

permits estimation of the time (x) in days that the soil-moisture tensions are less than (y) bars. Typical lengths of time of the two soils at 3 selected soil-moisture tensions are presented in Table 6.

Table 6. Time with soil moisture tensions less than indicated values for two soils.

Soil	Soil moisture tension-bars		
	0.3	1.0	7.0
	(days)	(days)	(days)
Sandy loam-Reno	1.4	5.0	10.7
Loam-Phoenix	4.6	5.4	6.8

With information on the rate of seed germination at selected soil-moisture tensions, it is possible to estimate the number of seeds that would germinate at the selected soil moisture regime and those temperature and radiation conditions.

Equation (1) is divided by the number of seeds planted (30 in the studies) and multiplied by 100.

$$y = [(A + B \ln\ (x))/\text{number of seeds}] \times 100 \qquad (4)$$

where y = expected seed germination in percent,
x = time in days that soil moisture is less than specified value from Equation (3), and
(A) and (B) = regression coefficients of seed germination at specified soil moisture tensions (Table 4).

Some expected germination percentages based on the results of the germination data of Lehmann lovegrass and blue panicgrass are presented in Table 7.

Table 7. Estimated germination percentages of Lehmann lovegrass and blue panicgrass on two soils as affected by soil water availability.

Soil	Species	Soil Moisture Tension-bars		
		0.3	1.0	7.0
		(%)	(%)	(%)
Sandy loam	Lehmann lovegrass	6.6	14.2	3.3
	Blue panicgrass	25.8	48.3	20.4
Loam	Lehmann lovegrass	24.2	14.8	2.7
	Blue panicgrass	62.3	50.2	17.2

This approach estimates only the effect of soil moisture tension on expected rate and total seed germination in the field. The soil data used in the previous discussion are presented only as an example for illustrating the technique. The soil-drying parameters must be derived under and be representative, of the climatic conditions and time of year that actual seed planting would be conducted. Other factors that must be considered are the effects of temperature and soil texture on seed germination. Finally, the survival of the germinated seeds and seedlings as affected by soil-water availability must be evaluated.

SUMMARY AND CONCLUSIONS

Available soil moisture is one of the key factors affecting seed germination. Information on the effects of soil moisture tensions on germination of range plant species has in the past been primarily derived from studies using solutions of salts or polyethylene glycol (PEG). These results may not be representative of field conditions.

Studies were conducted to develop information on the survival of germinated seeds at high soil water tensions. Germinated seeds of five warm-season grasses were placed on dry filter paper for periods of 1 to 10 days then rewetted to determine the number of seeds which survived. The results showed that sideoats grama was significantly more tolerant of the dry period following germination than were blue panicgrass or the three lovegrass species.

The rate of seed germination of the five grasses at four water-tension levels was evaluated on three soils. Germination was affected by soil-water tensions and not soil-water content. A technique was developed to relate the germination rate at reduced water-potentials to soil drying parameters for estimating the seed germination that might be expected in the field.

ACKNOWLEDGEMENT

LITERATURE CITED

Collis-George, N., and Jennifer B. Hector. 1966. Germination of seeds as influenced by matric potential and by the area of contact between seed and soil water. Aust. J. Soil Res. 4:145-164.

Collis-George, N., and Jocelyn E. Sands. 1962. Comparison of the effects of the physical and chemical components of soil water energy and seed germination. Aust. J. Agr. Res. 13:575-584.

Evans, Raymond A., and James A. Young. 1972. Germination and establishment of Salsola in relation to seedbed environment. II. Seed distribution, germination, and seedling growth of Salsola and microenvironmental monitoring of the seedbed. Agron. J. 61:219-224.

Frasier, Gary W., Jerry R. Cox and David A. Woolhiser. 1985. Emergence and survival response of seven grasses for six wet-dry sequences. J. Range Manage. 38:372-377.

Fulbright, Timothy E., A.M. Wilson and E.F. Redente. 1984. Effects of temporary dehydration on growth of green needlegrass (Stipa viridula Trin.) seedlings. J. Range Manage. 37:462-464.

Hassanyar, Amir S., and A.M. Wilson. 1978. Drought tolerance of seminal lateral root apices in crested wheatgrass and Russian wildrye. J. Range Manage. 31:254-258.

Hruschka, Howard W., 1973. Systematic application of Duncan's multiple range test to biological research data. ARS-NE-6. U.S. Department of Agriculture, Agricultural Research Service, Washington D.C. 13 pgs.

Hunter, J.R., and A.E. Erickson. 1952. Relation of seed germination to soil moisture tension. Agron J. 44:107-109.

Jackson, R.D., 1973. Diurnal changes in soil water content during drying. In Field Soil Water Regime. Pgs 37-35. Soil Science Society of America. Madison, Wisconsin.

Kaufmann, Merrill R., and Kathleen J. Ross. 1970. Water potential, temperature, and kinetin effects on seed germination in soil and solute systems. Amer. J. Bot. 57:413-419.

Nakayama, F.S., R.D. Jackson, B.A. Kimball and R.J. Reginato. 1973. Diurnal soil-water evapotranspiration: chloride movement and accumulation near the soil surface. Soil Sci. Soc. Amer. Proc. 37:509-513.

Sedgley, R.H., 1963. The importance of liquid seed contact during germination of Medicago tribuloides Desr. Aust. J. Agric. Res. 14:646-653.

Sharma, M.L., 1973. Simulation of drought and its effect on germination of five pasture species. Agron. J. 65:982-987.

Watt, L.A., 1978. Some characteristics of the germination of Queensland blue grass on cracking black earths. Aust. J. Agric. Res. 29:1147-1155.

Watt, L.A., 1982. Germination characteristics of several grass species as affected by limiting water potentials imposed through a cracking black clay soil. Aust. J. Agric. Res. 33:223-231.

Wilson, A.M., Jack R. Nelson and Carl J. Goebel. 1970. Effects of environment on the metabolism and germination of crested wheatgrass seeds. J. Range Manage. 23:283-288.

Young, James A., and Raymond A. Evans. 1972. Germination and establishment of Salsola in relation to seedbed environment. I. Temperature, afterripening, and moisture relations of Salsola seeds as determined by laboratory studies. Agron. J. 64:214-218.

Young, James A., Raymond A. Evans and Burgess L. Kay. 1970. Germination of cultivars of Trifolium subterraneum L. in relation to matric potential. Agron. J. 62:743-745.

ENVIRONMENT AND WATER PATTERN OVERRIDE AMOUNT FOR GRASS ESTABLISHMENT IN NORTH DAKOTA

Ronald E. Ries and Lenat Hofmann[1]

ABSTRACT

We evaluated establishment success of four grasses with increasing amounts of water. Increased water did not significantly increase stand densities. Effectiveness of the lower water amounts is explained by environmental conditions and pattern in which the water was received. Late seeding date and subsequent environmental conditions favored warm-season grass establishment.

INTRODUCTION

In the semiarid and arid West, water is the most important single factor influencing successful grass establishment. The amount, pattern, and timing of precipitation in western North Dakota determine the water available for establishing grass seedlings. Periods of drought are common and precipitation is often limited and very irregular (Ries and Day 1978). For this reason, precipitation is often insufficient to insure initial establishment of grasses. Studies (Ries et al. 1979; Ries 1980) have shown that water added by irrigation to supplement precipitation can be beneficial to successful grass establishment. However, in North Dakota where this practice usually is not necessary, it can protect against grass establishment failures when precipitation is low or irregular. This paper reports the establishment success of four grasses as affected by increasing amounts of water received after seeding.

STUDY METHODS

This study was conducted at the Northern Great Plains Research Laboratory, Mandan, ND on plots located under and outside a rainout shelter. Soils of the study area are a Parshall fine sandy loam (coarse-loamy, mixed Pachic Haploborolls). Plots were established on a tilled seedbed in a randomized complete block, split plot design with two replications. Main plots (6.0 by 7.6 m) were water treatments and sub plots (1.5 by 7.6 m) were grass species.

Three water treatments were used in this study: 1) natural precipitation received (15.16 cm for June, July, and August); 2) a dry year treatment (70% probability) (11.89 cm for June, July, and August); 3) a wet year treatment (20% probability) (30.96 cm for June, July, and August). The dry and wet water treatment plots were located under a rainout shelter (Ries and

Zachmeier 1985). The shelter would close over the plots when rainfall occurred. The total water needed to simulate the dry and wet years was divided by the total number of biweekly irrigation days in June, July, and August. The amount of water necessary for establishing the wet and dry year treatments was applied to the plots each Tuesday and Thursday with a rotating boom irrigator equipped with a flow meter. Plots that received naturally occurring precipitation were located next to the rainout shelter. Available soil water (4.5 cm) in the top 30.5 cm was near field capacity (4.9 cm) and essentially equal on all plots at the beginning of the study.

Four grass monocultures were used in the study: blue grama (Bouteloua gracilis [HBK.] Lag.), native collection; sideoats grama (Bouteloua curtipendula [Michx.] Torr.), 'Pierre'; crested wheatgrass (Agropyron desertorum [Fisch.] Schult.), 'Nordan'; and Russian wildrye (Psathyrostachys juncea [Fisch.] Nevski), 'Vinall'. These species were seeded at 11.2 kg/ha of pure live seed on June 21, 1982, at a depth of 1.3 cm. All species, except for blue grama, were seeded with a drill with depth bands, packer wheels, and a cone metered seeding mechanism for accurate seed amount and distribution in 15 cm row spacing. Blue grama was hand seeded and raked to cover the seed.

Precipitation, air temperature, free water evaporation, and soil water were monitored. Precipitation, air temperature, and free water evaporation were measured with standard U.S. Weather Bureau instruments and techniques. Soil water was monitored weekly by neutron access tubes to a depth 2 m in 30.5 cm intervals and gravimetric samples to a depth of 8 cm in 1.3 and 2.5 cm increments.

Stand characteristics, including plant density by quadrat counts taken on August 30, 1982, and basal area taken at 1.3 cm above the soil with a point frame on September 15, 1982, were used to evaluate seeding success. Data were analyzed by analysis of variance for water and species differences. The Waller-Duncan T test, (k = 100) was used to rank means.

RESULTS AND DISCUSSION

Environmental data during the study period are given in Table 1. Precipitation received during June and August, 1982 was below the long term average for those months. July precipitation was slightly above the long term average. Especially noteworthy is the amount of free water evaporation recorded during June, July and August, 1982. Actual free water evaporation for the three months was 16.8 cm less than the long term average and reflects a year of less atmospheric water demand than normally occurs.

Table 1. Environmental data during study.

	Jun '82	LTA[1]	Jul '82	LTA[1]	Aug '82	LTA[1]
	- - - - - - - cm - - - - - - -					
Pptn.[2]	5.6	8.5	6.3	6.1	3.3	4.3
Evap.[3]	9.3	19.1	17.8	23.0	18.6	20.4
	- - - - - - - °C - - - - - - -					
Ma Temp.[4]	22.2	24.5	28.9	28.9	25.6	27.8
Mi Temp.[5]	10.0	11.1	14.4	14.4	12.2	12.8
Me Temp.[6]	16.1	17.8	21.7	21.7	18.9	20.6

[1]Long Term Average (1915-1982)
[2]Monthly precipitation
[3]Monthly free water evaporation
[4]Monthly mean maximum air temperature
[5]Monthly mean minimum air temperature
[6]Monthly mean air temperature

Total water received during the study was 15.16, 11.89, and 30.96 cm for the natural precipitation, dry, and wet treatments, respectively (Table 2.). The dry treatment received 3.27 cm less than natural precipitation and the wet treatment received 15.80 cm more.

Table 2. Actual water received by water treatments.

Treatments	June'82	Jul'82	Aug'82	Total
	- - - - - - - cm - - - - - - -			
Pptn.	5.59	6.27	3.30	15.16
Dry	5.33	3.51	3.05	11.89
Wet	10.54	11.68	8.74	30.96

Except for basal area of Russian wildrye, no significant relationship was detected between density or basal area and amount of water received (Table 3.). The new grass stands had equal density and basal area even though actual water amounts received ranged from 11.89 cm (dry) to 30.96 cm (wet). Russian wildrye showed a significant increase in basal area under the dry treatment. Corresponding with this basal area increase was a decrease in weed competition.

Table 3. Stand density and basal area.

Species[1]	Treatment	Density	Ratio[2]	Basal area
		(plants m^{-2})		(%)
Bogr	Pptn.	692a[3]	0.34a	23a
	Dry	520a	0.26a	17a
	Wet	606a	0.30a	27a
	Avg.	606A[4]	0.30A	22A
Bocu	Pptn.	147a	0.31a	19a
	Dry	211a	0.45a	25a
	Wet	91a	0.19a	19a
	Avg.	150B	0.32A	21A
Agde	Pptn	26a	0.06a	3a
	Dry	26a	0.06a	4a
	Wet	26a	0.06a	7a
	Avg.	26B	0.06B	5B
Psju	Pptn.	4a	0.01a	1b
	Dry	39a	0.09a	11a
	Wet	22a	0.05a	5b
	Avg.	22B	0.05B	6B

[1]Bogr - blue grama; Bocu - sideoats grama, Agde - crested wheatgrass; and Psju - Russian wildrye
[2]Ratio = plants m^{-2} established/number of pure live seed seeded m^{-2}.
[3]Within species, means with same lower case letters are not significantly different in response to water treatments (Waller- Duncan T test, k = 100).
[4]Species means, averaged for all water treatments, with same capital letter are not significantly different (Waller-Duncan T test, k = 100).

Averaged for water treatments, blue grama had the greatest stand density by August 30, 1982 (606 plants m^{-2}). Sideoats grama had 150 plants m^{-2}. Both cool-season species--crested wheatgrass and Russian wildrye--had the fewest seedlings with 26 and 22 plants m^{-2}, respectively (Table 3). Averaged for water treatments, blue and sideoats grama established 30 and 32% of PLS seeded, respectively. This was statistically greater than for crested wheatgrass and Russian wildrye which established 6 and 5% of PLS seeded, respectively. Basal area taken on September 15, 1982, and averaged for water treatments showed both blue and sideoats grama had significantly greater basal areas than did crested wheatgrass and Russian wildrye.

Are there any plausible explanations for these results? First, available soil water was near field capacity on all plots at the beginning of this study. Furthermore, free water evaporation during the early part of this study, from seeding on June 21 through the end of July (fig. 1), was below average which optimized the efficiency of the low water treatments. Free water evaporation reflects the atmospheric water demand for establishing seedlings. The most

critical period for the warm-season grasses was
July 24-28 when the seedlings were making
maximum initial adventitious root growth. At
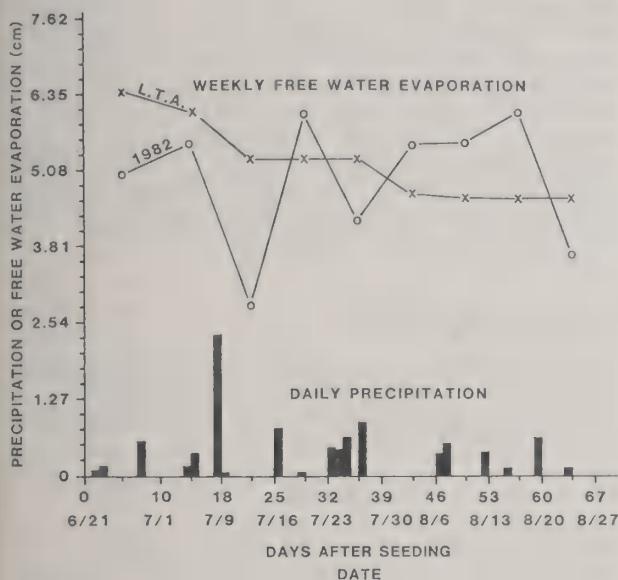this time free water evaporation was below
average (fig. 1).

Figure 1. Free water evaporation and
precipitation pattern during study.

Along with reduced free water evaporation,
natural and simulated precipitation were
received in a favorable pattern for grass
seedling establishment. Simulated precipitation
was applied evenly every Tuesday and Thursday by
irrigation which made four days the longest
period between watering. Several natural
rainfall events occurred during the critical
July 24-28 period for the warm-season grasses
with the longest interval between natural
rainfall events being nine days during late July
and early August (fig.1). Others have reported
a similar influence of water pattern and
environmental conditions on establishment of
warm-season grasses (Wilson and Briske 1979;
Frasier et al. 1987).

Finally, one would expect the favorable soil
water, low water demand, and favorable amount
and pattern of water to also be beneficial to
the cool-season species. This was not the case
in this study. The late planting date and
subsequent environmental conditions of this
study favored the establishment of the
warm-season species. Good stands of cool-season
grasses are are often achieved when seeding is
done in April and May when air temperatures
average 12 to 19°C, maximum; -1 to 6°C, minimum;
and 6 to 13°C, mean. Air temperatures from
planting, June 21, 1982, through July 23, 1982,
averaged 27-33°C, maximum; 13-16°C, minimum; and
20-24°C, mean. This 11-14°C increase in average
air temperature appears to result in decreased
cool-season grass establishment and was not

overcome by favorable water treatments. On the
other hand, the warm- season species responded
favorably to both higher temperatures and
favorable water conditions.

SUMMARY AND CONCLUSIONS

This study showed no significant increases in
seedlings established when increased water
amounts were applied after seeding. This is
encouraging because warm-season grass seedlings
in this study were established on water amounts
equal to or below average precipitation. This
further suggests that there are many factors
determining successful grass establishment other
than just amount of water. The planting date
and subsequent environmental conditions of this
study favored warm-season grass establishment
over that of cool-season grasses.

Even though this study was conducted during an
atypical year, the results have been useful in
planning for future grass establishment research
at Mandan. First, grass establishment must be
studied over several years. Second, the most
optimum planting date and associated
environmental conditions must be identified for
several different grass species.

LITERATURE CITED

Frasier, G. W., J. R. Cox, and D. A. Woolhiser.
1987. Wet-dry cycle effects on warm-season
grass seedling establishment. J. Range
Manage. 40(1):2-6.

Ries, R. E. 1980. Supplemental water for
establishment of perennial vegetation on
strip-mined lands. ND Farm Research
37(6):21-23.

Ries, R. E., and A. D. Day. 1978. Chapter 28--
Use of irrigation in reclamation in dry
regions. p. 505-520. In Reclamation of
Drastically Disturbed Lands. F. W.
Schaller and Paul Sutton (eds.). ASA,
CSSA, SSSA, Madison, WI.

Ries, R. E., R. F. Follett, F. M. Sandoval, and
J. F. Power. 1979. Planting date and
water affects initial establishment of
perennial vegetative communities. p.
899-905. In Ecology and Coal Resource
Development. Vol. II. Mohan K. Wali
(ed.). Pergamon Press, New York, NY.

Ries, R. E., and L. G. Zachmeier. 1985.
Automated rainout shelter for controlled
water research. J. Range Manage.
38(4):353-357.

Wilson, A. M., and D. D. Briske. 1979.
Survival and adventitious root growth of
blue grama seedlings on the Central
Plains. J. Range Manage. 32(3):209-213.

DIASPORES OF RANGELAND PLANTS: ECOLOGY AND
MANAGEMENT

D. Terrance Booth[1]

> "This is the seed, compact of God,
> Wherein all mystery is enfolded."
>
> Galbraith from 'On a Seed'

ABSTRACT

Seven functions are identified for
rangeland-plant diaspores and the importance of
these functions to seed germination and seedling
establishment is reviewed. Current technology
for sowing 'problem' diaspores is discussed.

INTRODUCTION

Unfolding the mysteries of the seed is an
enduring occupation of mankind. It has helped
us to appease our hunger, satisfy our curiosity,
and to enrich our environments. These goals
continue and bear upon the ultimate objectives
of this symposium. Of seed ecology, Heydecker
(1973) wrote "ingenious mechanisms often outwit
our teleological imagination." Having
determined "the" purpose or function of a thing,
we have overlooked related ecological questions
because the questions seemed naive (emphasis is
Heydecker's). Heydecker's statement applies to
the ecology of seed appendages and coverings.
Dispersal is commonly regarded as "the" function
of seed appendages. Yet other functions,
incorporating 'ingenious mechanisms', are
evident and are as important to seedling success
as dispersal.

"Disperse" is defined as "to scatter or cause to
become widely spread"; "disseminate" is defined
as "to sow, to spread, or send out freely" (Gove
1981) and connotes sowing of seed because of its
derivation from the Latin "semin" or "semen",
meaning seed. "Dispersal" is less restrictive
than "dissemination" and is appropriate to
describe the scattering of pollen, spores, and
reproductive organs besides seeds.

Disseminule has been defined as that portion of
the plant dispersed in reproduction (Baldwin
1942, Daubenmire 1968), which broadens the
meaning beyond that of seed dispersal and makes
disseminule synonymous with propagule.
"Diaspore" is defined (Gove 1981) as a
disseminule, especially one specialized for
dispersal. Like disseminule, diaspore is
derived from a word meaning seed, the Greek
"sporos". Diaspore has been used (Grubert 1974,
van der Pijl 1982, Peart 1984) in discussing the
ecology of dispersed reproductive units. This
paper will concentrate on ecological functions

of diaspores as seed-containing units, and on
methods for sowing these units. Sowing is used
here to include all assisted seed-dispersal
methods, as opposed to planting which infers
placement of seed in the soil.

The author's studies of Eurotia lanata (Pursh)
Moq.; [Ceratoides lanata (Pursh) J.T. Howell]
diaspores and seedlings have provided his
introduction to this area of ecology, which
explains the bias this paper has toward that
species. The various functions identified or
postulated for diaspores are by no means unique
to Eurotia; however the Eurotia diaspore does
appear to have mechanisms which operate in all
identified diaspore functions.

FUNCTIONS OF DIASPORES

Diaspores, then, are seeds, fruits, fruits with
attached structures, or even flowerheads
(Rhanterium epapposum, Oliv.) or whole aerial
plants (Salsola) with several to many seeds; if
in each case the unit is dispersed and is for
the purpose of reproduction. Plant parts
dispersed with the seed sometimes have
mechanical and/or chemical functions that
contribute directly to seed success. Evidence
of this is found by comparing seedling
establishment from diaspores and from threshed
seeds.

For example, threshing Eurotia and Haloxylon
articulatum (Cav.) Bge. (Hammada scoparia
Iljin) increases germination but reduces seedling
establishment (Booth 1982, Booth and Schuman
1983, Sankary and Barbour 1972). Thalen (1979)
acknowledged this might also be the case for
Haloxylon salicornicum (Moq.) Bge. Threshed
Danthonia penicillata (Labill) Palisat. seed
established 12 times fewer seedlings than the
intact diaspores (Simpson 1952). Similar
findings are reported for six species studied by
Peart (1979). And, threshing Kochia prostrata
(L.) Schrad. seed is reported to increase
abnormal germination (Romo and Haferkamp 1987).
Injury to seed embryos during threshing was only
one of several reasons for reduced establishment
from threshed Eurotia seed (Booth 1982, Booth
1984a, 1987a), was a minor element in reducing
Danthonia establishment (Simpson 1952), and was
not considered to be a factor in the case of
Haloxylon articulatum, Kochia prostrata (Sankary
and Barbour 1972, Romo and Haferkamp 1987) or in
Peart's (1979) studies. Instead, the reduced
establishment was attributed to loss of assisting
functions by the parts removed in threshing.

Besides the commonly recognized function of
seed dispersal, seed coverings and appendages
may interact with seed and environment in:
seed positioning, seed fixation (anchoring),
hydraulic conductivity, seed protection,
substance transfer to the embryo, and
regulation of seed respiration. The natural
operation of each of these functions should be
considered before sowing (or modifying for
sowing) diaspores of rangeland plants.

---

[1] Range Scientist, USDA-ARS, High Plains
 Grasslands Research Station, 8408 Hildreth Rd.,
 Cheyenne, Wyoming 82009.

Dispersal

The dispersal function of most diaspores is easily recognized and will not be extensively discussed here. Dispersal is the subject of several books, numerous papers and has been investigated in its various modes (i.e., wind, water, gravity, zoological, and self dispersal (Ridley 1930)], mechanics (Burrows 1973, Angspurger and Franson 1987), and ecological implications (Harper 1977, van der Pijl 1982). Our focus is of man as the disseminator; therefore other modes are bypassed so that (hopefully) the seed remains where it is sown. This latter is no minor point. To accomplish our goals, seed must not only be dispersed but must be fixed in place and not removed from the site by other agents of dispersal. When appendages are retained on diaspores because of desirable contributions to plant establishment, or because of the difficulty of removing them without damaging the seed, seed fixation at sowing must overcome the dispersal function.

Seed Positioning

The position of the seed on, or in, the soil affects water uptake and contact of the radicle with the soil. Sheldon and Burrows (1973) and Sheldon (1974) found the pappus of a Composite achene could cause the basal attachment scar to be the first part of the seed to enter cracks and crevices of the soil surface. Sheldon (1974) further demonstrated, for some species, that water uptake was through the attachment scar and subsequently through the micropyle; which is evidence that seed position affects germination.

Positioning effects were also demonstrated by Stevens et al. (1986) for Chrysothamnus nauseosus (Pallas) Britt. ssp. albicaulis (Nutt.) Rydb. They studied 12 seed positions in and on the soil and found that position significantly affected the number of seedlings existing 30 days after planting. The evidence from other plant species is similar. Better establishment from whole diaspores of Danthonia, measured six months after sowing, was attributed to seed positioning by the awn (Simpson 1952). The flat side of diaspores of Panicum turgidum Forsk. appears to be a positioning adaptation for improved water uptake that increases germination (Koller and Roth 1963). Positioning appendages in the form of unicellular hairs on the testa are reported for Blepharis persica (Burm.) Kuntze. (Gutterman et al. 1967). When Blepharis diaspores fall on wet ground and touch soil with their flat sides, hydration and swelling of the hairs raise the seeds to an angle of 30-45 degrees to the soil surface, bringing the micropyle into contact with the soil. This allows imbibition leading to germination.

The manner in which an appendage affects seed position has also been used to explain the relative success of different species on different soils; the result of seed position on water uptake and on soil penetration by emerging radicles is cited as critical factors in differential establishment (Harper et al. 1970, Harper 1977, Peart 1979).

Besides seed orientation for water uptake and for immediate radicle penetration, positioning by appendages can also be regarded as influencing vertical location in relation to the soil surface (planting depth), though this is also related to fixation.

Fixation (Anchoring)

Fixation holds seeds in place so agents of dispersal cease to move them about; and, fixing counterbalances the resistance of the soil to radicle penetration. This enhances, or makes possible, radicle entry. Stolzy and Barley (1968) have discussed the forces involved during soil penetration by the radicle and Taylor and Gardner (1960) demonstrated fixation was necessary for maximum transmission of growth pressure to the penetrating root.

Fixation by burial gives seeds some protection against rapid water loss, extreme temperatures, depredation, and fire (Harper 1977, Peart 1984) and assures emerging radicles enter the soil. However, the need to raise photosynthetic tissue through covering materials imposes limitations on initial shoot morphology and on minimum seed reserves. The latter seems to also influence total numbers of diaspores produced. These limitations may explain why adaptations to surface, or near surface, germination are extremely common (Harper 1977).

Wind dispersed diaspores are often fixed by anchoring connections formed between appendages and soil. Examples are the long bract-hairs of Eurotia (Booth 1982, Booth and Schuman 1983), the diaspore wings of Haloxylon articulatum (Sankary and Barbour 1972), and the pappus of Chrysothamnus (Stevens et al. 1986). These reports all note the importance of anchoring to radicle penetration.

Mucilaginous anchoring is common in species from dry climates and can be especially effective in fixing seeds to soil surfaces (Young and Evans 1973, Grubert 1974). Mucilage may cover diaspores or be excreted from special cells in the seed coat (Harper and Benton 1966, Grubert 1974, Mayer and Poljakoff-Mayber, 1982). Mucilage also forms from appendages (Grubert 1974), a phenomenon which has been described, with the attendant benefit to radicle penetration, for Blepharis (Gutterman et al. 1967) and noted for some species of Senecio (Grubert 1974, Harper 1977). Diaspores which become mucilaginous upon wetting are referred to as myxospermic. Young and Evans (1973) have surveyed for myxospermic species in the western portion of the Great Basin and Grubert (1974) extensively reviewed myxospermy in Angiospermae.

Another common phenomenon of arid-land species

is the hygroscopic action of diaspore appendages like those of Avenae, Cercocarpus, Erodium, Stipa, and others. These actions cause diaspores to creep and hop across soil surfaces until lodged in cracks or other safe sites (Harper et al. 1965, Harper 1977, Peart 1979), or to bore into the soil [Zohary (1937) for 48 species; as cited by van der Pijl 1982, Young et al. 1975 for Erodium botrys (Cav.) Bertol]. Backwardly-directed bristles, barbs, and teeth fix these diaspores in place (Sheldon 1974, Peart 1979) and counter soil resistance to radicle penetration (Peart 1979, 1981, 1984).

Fixation by litter cover is important in the ecology of several annual plants (Evans and Young 1970), and like other methods of fixation, improves radicle penetration into the soil by holding surface-lying seeds in place [Salsola kali var. tenuifolia Tausch (Salsola iberica Sennen and Pau) Evans and Young 1972]. Litter fixation is a likely phenomenon for most tumbleweeds and other aggregating diaspores.

Hydraulic Conductivity

Hydraulic conductivity at the diaspore-soil interface is closely related to anchoring and to positioning. Adhesion to soil by hairs, pappus, awn or mucilage improves water conductivity (Young et al. 1970) by increasing the amount of surface area available for water absorption, and the intimacy of soil particles and absorbing surfaces (Harper and Benton 1966, Hadas and Russo 1974a, 1974b, Bewley and Black 1978). The effect of diaspore characteristics on water absorption by seeds has been studied using an assortment of seeds of different sizes and shapes, with and without mucilage and tested under various degrees of water tension (Harper and Benton 1966, Young et al. 1970, Harper 1977). Enhanced hydraulic conductivity by seed appendages is particularly beneficial to species where water absorption is not restricted to one portion of the diaspore or to the micropyle of the seed.

Protection

Diverse characteristics of diaspores provide protection to seeds and new seedlings. Protection against physical injury is one aspect (Stevens et al. 1977, Sankary, and Barbour 1972). Secondary plant products such as the cucurbitacin D of the Purshia tridentata (Pursh) DC. seed have been shown to inhibit some insect predation (Dreyer and Trousdale 1978, Jermy et al. 1981). Deacetoxymatricarin from Artemisia tridentata Nutt. branches and unidentified compounds from Chrysothamnus nauseosus branch ends were also shown to repel some insects (Jermy et al. 1981). While only branch ends of Artemisia and Chryosthamnus were tested for the repellent chemicals, it is possible that these species, like Purshia, have the respective chemicals throughout the plant, including the diaspores. A similar protective function may occur with arils, which are outgrowths or

appendages of seeds that frequently contain chemical compounds not found elsewhere in the plant (Bewley and Black 1978).

Thick coats on large seed may protect against predation (Fenner 1983) and awns and spines may reduce herbivory (Smith 1968). Injury to livestock by diaspores of plants like Aristida, Bromus, Hordeum and Stipa is well documented (US Forest Serv. 1937, Stoddart and Smith 1955, Smith 1968). That these injuries or the threat of injury actually cause grazing animals to avoid the diaspores has been questioned (van der Pijl 1982). However, a study of the botanical composition of cattle diets in Wyoming provides evidence that cattle do avoid awns of Stipa comata Trin and Rupr. (Samuel and Howard 1982). It seems reasonable that similar structures of other plants could have similar effects.

Not all decimating factors are biological, and certain diaspore characteristics can be identified which improve the microclimate of seeds or seedlings during adverse environmental conditions. The bracts of Eurotia diaspores reduce precocious germination of the seed (Stevens et al. 1977, Booth and Schuman 1983) and the wings of Haloxylon articulatum appear to reduce dessication hazards (Sankary and Barbour 1972). The fluffy hairs on Eurotia bracts also cause shed diaspores to collect into groups; Murbeck called it synaptospermy (1919/20 as cited by van der Pijl 1982) and described it as a situation in which the diaspore complex absorbed more moisture and held moisture against loss to evaporation better than isolated seeds. Woodmansee and Potter (1971) have described the accumulation of Eurotia diaspores in depressions and the importance of sheltering material to seedling survival. Piles of Salsola and other tumbleweeds in ditches and along fences are manifestations of the same phenomenon. The complex of accumulated plant material offers protection against environmental extremes (Evans and Young 1970, 1972) which apparently compensates for increased competition.

Transfer of Substances

Most literature on this subject deals with germination inhibitors that move to the embryo from appendages and coverings (Koller 1957, Nord and Van Atta 1960, Ahring et al. 1975, Ansely and Abernethy 1985). The resulting seed dormancy presents significant problems in the culture of rangeland plants.

Inhibitors, however, are not the only substances transferred. Eurotia seeds from diaspores imbibed in deionized water were significantly higher in calcium and magnesium than the preimbibed seed (Booth 1985a, 1987a). This influx of cations has been shown to improve seed imbibition (Booth 1987b), seed germination (Hilton 1941, Booth 1987b), and seedling growth (Booth 1985a, 1987a). Similar findings are reported for Sarcobatus

vermiculatus (Hook) Torr. (Romo and Eddleman 1985, Eddleman and Romo 1987) and are suggested for Kochia prostrata (Romo and Haferkamp 1987). Therefore substances transferred to the embryo from appendages and coverings may hinder or may assist propagation of the plant.

Regulation of Respiration

Seed coverings may impose seed dormancy by preventing – or significantly limiting – oxygen from reaching the seed embryo (Thornton 1945, Kozlowski and Gentile 1959, Mayer and Poljakoff-Mayber 1982). Removing or abraiding these coverings, as in the case of Oryzopsis hymenoides (Roem. and Schult.) Ricker (Fendall 1964, Zemetra et al. 1983), probably overcomes dormancy by increasing seed respiration. Thus, seed respiration in the diaspore may be regulated by oxygen flow through seed coverings.

Different examples of this phenomenon occur with mucilage layers around seeds, which when swelled with too much water may restrict gas exchange by the embryo (Gutterman et al. 1967, van der Pijl 1982). Similarly, germination of Eragrostis lehmanniana Nees. is improved by treatments which abrade or loosen the gelatinous coating around the seed (Haferkamp et al. 1977).

Conversely, too much oxygen may negatively affect seedling vigor by uselessly increasing the respiration rate and wasting seed reserves. Thalen (1979) found the weight of husked diaspores of Haloxylon salicornicum decreased with time. Booth (1987b) found dry weights of ten-day-old Eurotia seedlings were significantly higher from whole diaspores than from threshed seed. This difference might be partly due to the effect of the bracts in limiting uncoupled respiration by the seed during imbibition. Both situations suggest threshing caused an undesirable increase in seed respiration.

Application of Seedbed Ecology

Those who use and deal with seeds, particulary seeds with appendages and coverings, need to be aware of all diaspore functions. If awns, hairs, bracts, or other parts are modified prior to sowing, will the modification interfere with, or improve, seedling establishment and survival? For each species, propagators should consider diaspore functions and options for compensating and/or assisting the natural potential for seedling establishment.

SOWING DIASPORES

Introduction

Diaspore forms and functions vary by species. Management, that is presowing treatments and methods of sowing, should reflect that variation and the specific adaptations of each

plant. Diaspore management may mean threshing seeds from their coverings to promote germination; or implementing new technology, such as fluid drilling, to sow intact diaspores and use to advantage a growth promoting relationship between seed and appendages. Diaspores that are fluffy, hairy, awned or otherwise incompatible with standard drills, or that are adapted to surface germination and require assisted fixation to keep the seed in place, pose special problems in mechanized sowing. This section will discuss current technology for sowing 'problem' diaspores.

Special Drills

Seed drills were developed to plant slick seed; other kinds of diaspores, especially those with appendages, may jam or bridge the drop holes (Pellant and Reichert 1984). The development of metering devices that will handle fluffy seed, and their incorporation into commercial drills (Wiedeman and Cross 1981, Wiedeman 1982) has greatly improved this situation. These drills give us the capability to uniformly disperse appendaged seed and place it in the soil at an appropriate depth, or broadcast it on the surface.

The effect of planting depth on establishment of surface germinating rangeland species has been investigated for Eurotia (Booth 1987b, for a review of studies), Acacia schaffneri (S. Wats.) F.J. Herm. (Everitt 1983a), Acacia rigidula Benth. (Everitt 1983b) Kochia scoparia (L.) Schrad. (Everitt et al. 1983), and Kochia prostrata (Stevens and Van Epps 1984). Burying these species had an effect similar to planting any species too deeply. The number of plants emerging was inversely related to planting depth. Deep planting results in (1) lower total emergence, (2) lower rate of emergence, and (3) poor root development [Black 1956 for Trifolium subterraneum L., Fulbright et al. 1985 for Stipa viridula (Trin.)]. Rapid germination and emergence and rapid root and shoot growth in early stages of development are important to competitive ability (Black and Wilkinson 1963, Guneyli et al. 1969). The indications of reduced vigor and the questionable survival rate of seedlings from deeply planted seed justifies a cautious attitude toward covering seeds adapted to surface germination.

Broadcasting

The practice of broadcast sowing has increased with passage of reclamation laws requiring species diversity and with the emphasis on native plants. In some cases broadcasting has been the only practical method, either because of the terrain or because of "trashy seed" (Ries and DePuit 1984). DePuit and Coenenberg (1979) found broadcasting small seeds was better than drilling them 2.5 cm into the soil. However, as a means for sowing seeds adapted to burial, broadcasting is, at best, inefficient in terms of established

plants to sown seed (Wood et al. 1982, Herbal 1986). Broadcasting does not fix seeds. Seeds may be removed from the sown area by various modes of dispersal (Parady 1985) and/or plant establishment reduced because fewer radicles penetrate the soil surface. Seedbed treatments that disturb the soil surface before or after broadcasting do increase the number of fixed seeds and often give satisfactory results (Luke and Monsen 1984, Herbal 1986). (For a review of broadcasting seeders see Larson 1982).

There is room for improvement in broadcasting techniques, especially with regard to sowing diaspores of surface adapted species. Areas of potential progress are: (1) surface modifications, such as those to better accommodate creeping and lodging diaspores, (2) use of fluid and solid carriers to enhance fixation of broadcast units (see subsequent sections) and (3) timing, to use impending precipitation events or saturated seedbeds to increase the number of diaspore appendages that become embedded in the soil.

Spreading Hay

Sowing plants by spreading mature hay can be a practical and economical method of plant establishment if good sources of seed-containing hay can be obtained (Wenger 1941, Gates 1962). The method has been used to establish a number of grasses and forbs and has also been recommended as one method of sowing Eurotia (Ries et al. 1980, Wasser 1945). Seed fixation occurs largely because of the litter cover which is itself anchored by crimping. Microclimate moderation and soil protection are additional benefits of using hay.

Snowbank Seeding

Some work has been done with sowing through or onto accumulated snow. Eurotia diaspores dropped onto the soil surface through 4 cm diameter holes punched in 30 to 60 cm of snow established 25% of the pure live seed (PLS) sown (Booth 1987b). The bottom of a snowbank is a protected site where fixation readily occurs and moisture is not limiting; however, without mechanized equipment the method is labor intensive and slow.

Polyvinyl Alcohol Tape

The tape is made by placing diaspores between two strips of polyvinyl alcohol film[1]. Upon contact with moisture the film begins to dissolve and forms a viscous mass which glues diaspores to the soil surface, in effect duplicating a natural form of fixation. In test plots in Wyoming, tapes have given the highest rates of establishment (29% of PLS) of all methods tried for Eurotia (Booth 1987b). Shaw and Monsen (1984) note tapes are one way to sow and space plants in a nursery. Although seed tapes are common in the horticulture industry, the author is not aware of any commercial companies that currently tape diaspores for rangeland sowing. Hand production of tapes is expensive.

Pelleting

Pelleting of hairy or fluffy diaspores reduces clinging and it makes mechanical dispersal easier and more uniform. A properly functioning pellet anchors the diaspore in place as it dissolves. Andropogon gerardii var paucipilus (Nash) Fern., Cenchrus cilaris L., Eurotia and Schizachyrium scoparium (Michx.) Nash. have been pelleted for rangeland sowing. The method has been judged successful with regard to mechanical distribution of the diaspores[2] (Pogue 1983, Kocher and Stubbendieck 1986) and Kocher and Stubbendieck (1986) have shown pelleting did not reduce seedling establishment. Pelleting triples the weight of the Eurotia diaspore and pelleting charges are based on the finished weight[3]. It is recommended that diaspores be pelleted as close as possible to the planting date to avoid breakdown of pellets during storage.

Pellets of hydrophilic coatings to attract and hold water around seeds did not increase the germination or emergence of Elymus junceus Fisch. (Berdahl and Barker 1980), nor is water retention a function of natural seed mucilages (Grubert 1974). Various other methods of seed pelleting and coating have been tried with range grasses adapted to burial, and have not been successful (Hull 1959, Vallentine 1971).

---

[1]Polyvinyl alcohol film is produced by Chris*Craft Industrial Products, Inc. of Gary, Indiana. Mention of commercial companies and their products is for information only and does not imply endorsement.
[2]Personal communication Mike Pellant, Bureau of Land Management. Boise, Idaho.
[3]Personal communication Stuart Barclay, CelPril Industries, Inc., Manteca, California. Mention of commercial companies and their products is for information only and does not imply endorsement.

Hydroseeding

Pellant and Reichert (1984) have reported the use of a hydroseeder to sow Eurotia diaspores with a mixture of grass seed. Hydroseeding overcame problems of bridging and seed separation encountered with other machines, and it allowed the operator to select good microsites, as opposed to uniformly sowing all landscape surfaces. Diaspore distribution was uniform within planted areas. The method was labor intensive and required large quantities of water be hauled to the field site. Stand establishment was not measured.

Fluid Drilling (Gel Seeding)

The suspension of diaspores in a hydrocolloidal gel overcomes the problem of synaptospermy and, as with tape, fixes diaspores to the soil surface in a manner similar to natural mucilage (Booth 1984b). Unlike taping and pelleting, mixing diaspores into a gel is not time consuming nor does it require highly specialized equipment. Moreover, planting equipment is commercially available or can be fabricated (Ghate et al. 1981, Booth and Griffith 1986).

Fluid drilling does not damage soft seeds and can be used to sow preimbibed and pregerminated diaspores. This is especially important for those species where water uptake is restricted by seed coverings or where natural stratification is a problem (Booth 1985b). Apparent advantages of sowing pregerminated diaspores of rangeland plants is greatly complicated by wide germination spans inherent in seedlots of many wildland species (Morgan and Booth, unpublished data). However, osmotic pretreatment may synchronize germination of some of these species (Bradford 1986, Morgan and Booth 1987).

Eurotia establishment from fluid drilling has not been as successful as other sowing methods tested in Wyoming (Booth 1984b). The best establishment was 11% of PLS after it was sown through a 5-7 cm spring snowfall using a compressed-air gel seeder (Booth and Griffith 1986, Booth 1987b). It appears that desiccation and depredation are serious problems encountered when fluid drilling surface-germinating species.

SUMMARY

The appendages and seed coverings of diaspores have traditionally been regarded as mechanisms for dispersal and have been removed from seeds if they interfered with mechanical planting. However, besides the well recognized function of seed dispersal; diaspores also protect, position, and fix (anchor) seeds. They improve hydraulic conductivity, effect the transfer of substances to the embryo, and regulate seed respiration. These functions contribute as much to the success of a species as dispersal and, like dispersal, can be managed by man to increase seedling establishment and improve seedling vigor. Good management requires (1) an understanding of the mysteries of specific seedbed ecologies and (2) innovation in adapting methods of seed distribution and fixation that will complement, rather than contradict, those diaspore functions most critical to seed success.

LITERATURE CITED

Ahring, R.M., J.D. Easton, and C.S. Garrison. 1975. Seed appendages and germination of two Asiatic bluestems. Agron. J. 67:321-325.

Ansley, R. James, and Rollin H. Abernethy. 1985. Environmental factors influencing Gardner saltbush seed dormancy alleviation. J. Range Manage. 38:331-335.

Augspurger, Carol K., and Susan E. Franson. 1987. Wind dispersal of artificial fruits varying in mass, area and morphology. Ecology 68:27-42.

Baldwin, Henry Ives. 1942. Forest tree seeds. Chronica Botanica Co. Waltham, Miss. USA

Berdahl, J.D., and L.E. Barker. 1980. Germination and emergence of Russian wildrye seeds coated with hydrophilic materials. Agron. J. 72:1006-1008.

Bewley, J.D., and M. Black. 1978. Physiology and biochemistry of seeds. Vol. I. Springer-Verlag, New York.

Black, J.N., and G.N. Wilkinson. 1963. The role of time of emergence in determining the growth of individual plants in swards of subterranean clover (Trifolium subterraneum L.) Aust. J. Agric. Res. 14:628-638.

Black, J.T. 1956. The influence of seed size and depth of sowing on pre-emergence and early vegetative growth of subterranean clover (Trifolium subterraneum L.). Aust. J. Agric. Res. 7:98-109.

Booth, D. Terrance. 1982. The ecological, physiological and morphological effects of threshing winterfat fruits. p. 133-137. In: Earl F. Aldon and Wendall R. Oaks (eds.) Proc. 'Reclamation of Mined Lands in the Southwest' a symposium, October 20-22. Albuquerque, NM. Soil Conserv. Soc. of Amer.

Booth, D. Terrance. 1984a. Threshing damage to radicle apex affects geotropic response of winterfat. J. Range Manage. 37:222-225.

Booth, D. Terrance. 1984b. Innovation in wildland shrub establishment. Minerals and the Environment. 6:111-114.

Booth, D. Terrance. 1985a. Calcium and magnesium content of winterfat seedlings cultured at cold temperatures. Abstr. of Papers. 38th meeting. Soc. Range Manage. (Salt Lake City, Utah). Abstr. 159.

Booth, D. Terrance. 1985b. Fluid drilling (gel seeding) for wildland plantings: some preliminary studies. 49-53. In: Thomas D. Landis (compiler). Proc.: Western forest nursery council - Intermountain Nurseryman's Association Combined meeting, 1984 August 14-16; Coeur d'Alene, Idaho. General Technical Report INT-185. Ogden, UT: USDA Forest Serv. Intermountain Res. Sta.

Booth, D. Terrance. 1987a. The winterfat fruit. Abstr. of Papers. 40th meeting. Soc. Range Manage. (Boise, Idaho). Abstr. #119.

Booth, D. Terrance 1987b. Contributions to the reproductive autecology of winterfat [Eurotia lanata (Pursh) Moq.] with notes on direct seeding methods. Ph.D. Dissertation. Univ. of Wyoming, Laramie, WY.

Booth, D.T., and L.W. Griffith. 1986. Small compressed-air gel seeder. Abstr. of Papers. 39th meeting. Soc. Range Manage. (Kissimmee, Florida). Abstr. 128.

Booth, D. Terrance, and Gerald E. Schuman. 1983. Seedbed ecology of winterfat: fruits versus threshed seeds. J. Range Manage. 36:387-390.

Bradford, Kent J. 1986. Manipulation of seed water relations via osmotic priming to improve germination under stress conditions. Hort Sci. 21:1105-1112.

Burrows, F.M. 1973. Calculation of the primary trajectories of plumed seeds in steady winds with variable convection. New Phytol. 72:647-664.

Daubenmire, Rexford. 1968. Plant Communities. Harper and Row Publ. New York.

DePuit, Edward J., and Joe G. Coenenberg. 1979. Methods for establishment of native plant communities on topsoiled coal stripmine spoils in the northern Great Plains. Reclamation Review. 2:75-83.

Dreyer, David L., and Eugene K. Trousdale. 1978. Cucurbitacins in Purshia tridentata, Phytochemistry 17:325-326.

Eddleman, L.E., and J.T. Romo. 1987. Sodium relations in seeds and seedlings of Sarcobatus vermiculatus. Soil Sci. (In Press).

Evans, Raymond A., and James Young. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. Weed Sci. 18:697-703.

Evans, Raymond A., and James A. Young. 1972. Germination and establishment of Salsola in relation to seedbed environment. II. Seed distribution, germination, and seedling growth of Salsola and microenvironmental monitoring of the seedbed. Agron. J. 64:219-224.

Everitt, J.H. 1983a. Seed germination characteristics of two woody legumes (Retama and Twisted Acacia) from South Texas. J. Range Manage. 36:411-414.

Everitt, J.H. 1983b. Seed germination characteristics of three woody plant species from south Texas. J. Range Manage. 36:246-249.

Everitt, J.H., M.A. Alaniz, and J.B. Lee. 1983. Seed germination characteristics of Kochia scoparia. J. Range Manage. 36:646-648.

Fendall, Roger K. 1964. An investigation into the site and cause of seed dormancy of Stipa viridula and Oryzopsis hymenoides Ph.D. Dissertation. NDSU Fargo, N. Dakota.

Fenner, M. 1983. Relationships between seed weight, ash content and seedling growth in twenty-four species of compositae. New Phytologist 95:697-706.

Fulbright, Timothy E., A.M. Wilson, and Edward F. Redente. 1985. Green needlegrass seedling morphology in relation to planting depth. J. Range Manage. 38:266-270.

Gates, Dillard H. 1962. Revegetation of a high-altitude, barren slope in northern Idaho. J. Range Manage. 15:314-318.

Ghate, S.R., S.C. Phatak, and C.A. Jaworski. 1981. Seeding pre-germinated vegetable seeds in plots. Trans. Amer. Soc. Agri. Eng. 24:1099-1102 and 1107.

Gove, Philip Babcock, editor. 1981. Webster's Third New International Dictionary of the English language - unabridged. Merriam-Webster Inc., Publishers. Springfield, Mass.

Grubert, M. 1974. Studies on the distribution of myxospermy among seeds and fruits of angiospermae and its ecological importance. Acta. Biol. Venez. 8:315-551.

Guneyli, E., O.C. Burnside, and P.T. Nordquist. 1969. Influence of seedling characteristics on weed competitive ability of sorghum hybrids and inbred lines. Crop Sci. 9:713-716.

Gutterman, Y., A. Witztum, and M. Evenari. 1967. Seed dispersal and germination in Blepharis persica (Burm.) Kuntze. Israel J. of Bot. 16:213-234.

Hadas, A., and D. Russo. 1974a. Water uptake by seeds as affected by water stress, capillary conductivity and seed-soil water contact. I. Experimental study. Agron. J. 66:643-647.

Hadas, A., and D. Russo. 1974b. Water uptake by seeds as affected by water stress, capillary conductivity and seed-soil water contact. II. Analysis of experimental data. Agron. J. 66:647-652.

Haferkamp, Marshall R., Gilbert L. Jordan, and Kaosu Matsuda. 1977. Pre-sowing seed treatments, seed coats, and metabolic activity of Lehmann lovegrass seeds. Agron. J. 69:527-530.

Harper, J.L, J.T. Williams, and G.T. Sagar. 1965. The behavior of seeds in soil I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. of Ecology 53:273-286.

Harper, John L., and R.A. Benton. 1966. The behavior of seeds in soil II. The germination of seeds on the surface of a water supplying substrate. J. of Ecology 54:151-166.

Harper, John L. 1977. Population biology of plants. Academic Press. New York.

Harper, J.L. P.H. Lovell, and K.G. Moore. 1970. The shapes and sizes of seeds. pp. 327-356. In: Johnston, Richard F. et al. (eds). Annual Review of Ecology and Systematics. Vol. I. Annual Reviews Inc. 4139 El. Camino Way, Palo Alto, Calif. USA.

Herbel, C.H. 1986. Seeding shrubs in the field. Reclam. and Reveg. Res. 5:377-385.

Heydecker, W. 1973. Seed ecology. pp. 1-3. In: W. Heydecker (ed.) Seed Ecology-proceedings of the Nineteenth Easter School in Agricultural Sciences. Univ. of Nottingham. 1972. Penn State Univ. Press. Univ. Park and London.

Hilton, J.W. 1941. Effects of certain micro-ecological factors on the germinability and early development of Eurotia lanata. Northwest Sci. 15:86-92.

Hull, A.C. Jr. 1959. Pellet seeding of wheatgrasses on southern Idaho rangelands. J. Range Manage. 12:155-163.

Jermy, Tibor, B.A. Butt, L. McDonough, David L. Dreyer, and Allan F. Rose. 1981. Antifeedants for the Colorado potato beetle I. antifeeding constituents of some plants from the sagebrush community. Insect Sci. Application 1:237-242.

Kocher, Eric, and J. Stubbendieck. 1986. Broadcasting grass seed to revegetate sandy soils. J. Range Manage. 39:555-557.

Koller, Dov. 1957. Germination-regulating mechanisms in some desert seeds, IV. Atriplex dimorphostegia Kar. Et. Kir. Ecology 38:1-13.

Koller, D., and Nurit Roth. 1963. Germination-regulating mechanisms in some desert seeds VII. Panicum turgicum (gramineae). Israel J. Bot. 12:64-73.

Kozlowski, Theodore T., and Arthur C. Gentile. 1959. Influence of the seed coat on germination, water absorption, and oxygen uptake of eastern white pine seed. Forest Sci. 5:389-395.

Larson, John. 1982. History of the vegetative rehabilitation and equipment workshop (VREW) 1946-1981. USDA Forest Serv. Equipment Development Center. Missoula, Montana.

Luke, F., and S.B. Monsen. 1984. Methods and costs for establishing shrubs on mined lands in southwestern Wyoming. p.286-291. In: Arthur R. Tiedemann et al. (compilers) Proceedings-- symposium on the biology of Atriplex and related chenopods; 1983 May 2-6; Provo, Ut. General Technical Rep. INT-172. Ogden, Ut: USDA, Forest Serv., Intermountain Forest and Range Exp. Sta.

Mayer, A.M., and A. Poljakoff-Mayber. 1982. The germination of seeds. 3rd Ed. Pergamon Press. New York.

Morgan, D.R., and D.T. Booth. 1987. The effect of osmotic priming on germination characteristics of four woody plant species. Abstr. of Papers. 40th meeting. Soc. Range Manage. (Boise, Idaho). Abstr. #143.

Murbeck, S. 1919/20. Beitrage zur biologie der Wustenpflanzen, I, II. Lunds Univ. Arsskr 15(10), 17(1).

Nord, Eamor C., and George R. Van Atta. 1960. Saponin - a seed germination inhibitor. Forest Sci. 6:350-353.

Parady III, Fred E. 1985. Reclamation equipment and techniques in southwestern Wyoming. In: 39th Annual Report. Vegetative Rehabilitation and Equipment Workshop. U.S. Forest Serv. Equipment Development Center. Missoula, MT.

Peart, Martyn H. 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. J. of Ecol. 67:843-863.

Peart, Martyn H. 1981. Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. J. of Ecol. 69:425-436.

Peart, Martyn H. 1984. The effects of morphology, orientation and position of grass diaspores on seedling survival. J. of Ecol. 72:437-453.

Pellant, M., and L. Reichert. 1984. Management and rehabilitation of a burned winterfat community in southwestern Idaho. p. 281-285. In: Arthur R. Tiedemann et al. (compilers) Proc.--symposium on the biology of Atriplex and related chenopods; 1983 May 2-6; Provo, Ut. General Technical Report INT-172. Ogden, Ut: USDA, Forest Serv., Intermountain Forest and Range Exp. Sta.

Pijl, L., van der. 1982. Principles of dispersal in higher plants. Springer-Verlag. New York.

Pogue, Gary. 1983. Flame-Coat[R] seed treatment process. p. 65-68. In: Harold T. Widemann and J.F. Cadenhead (compilers). Proc.--symposium on range and pasture seeding in the Southern Great Plains. Texas A&M University Agric. Res. and Ext. Center. Vernon, Tx.

Ridley, H.N. 1930. The dispersal of plants throughout the world. Reeve and Co. Ltd. Ashford.

Ries, R.E., and E.J. Depuit. 1984. Perennial grasses for mined land. J. Soil and Water Conserv. 39:26-29.

Ries, R.E., L. Hofmann, and W.C. Whitman. 1980. Potential control and value of seeds in prairie hay for revegetation. Reclam. Review. 3:149-160.

Romo, James T., and Lee E. Eddleman. 1985. Germination response of greasewood (Sarcobatus vermiculatus) to temperature, water potential and specific ions. J. Range Manage. 38:117-120.

Romo, James T., and Marshall R. Haferkamp. 1987. Forage kochia germination response to temperature, water stress, and specific ions. Agron. J. 79:27-30.

Samuel, Marilyn J., and Gene S. Howard. 1982. Botanical composition of summer cattle diets on the Wyoming High Plains. J. Range Manage. 35:307-308.

Sankary, Mohamed Nazir, and Michael G. Barbour. 1972. Autecology of Haloxylon articularum in Syria. J. of Ecology 60:697-711.

Shaw, Nancy, and Stephen B. Monsen. 1984. Nursery propagation and outplanting of bareroot chenopod seedlings. p. 251-260. In: Arthur R. Tiedemann et al. (compilers) Proc.--symposium on the biology of Atriplex and related chenopods; 1983 May 2-6; Provo, Ut. General Technical Rep. INT-172. Ogden, UT: USDA Forest Serv. Intermountain Forest and Range Exp. Sta.

Sheldon, J.C., and F.M. Burrows. 1973. The dispersal effectiveness of the achene-pappus units of selected compositae in steady winds with convection. New Phytol. 72:665-675.

Sheldon, J.C. 1974. The behavior of seeds in soil III. The influence of seed morphology and the behavior of seedlings on the establishment of plants from surface-lying seeds. J. of Ecology 62:47-66.

Simpson, Margaret. 1952. Value of the awn in establishing seed of Danthonia penicillata (Labill.) Palisot, N.Z. J. Sci. and Technology 34:360-365.

Smith, D.F. 1968. The growth of barley grass (Hordeum leporinum) in annual pasture 1. Germination and establishment in comparison with other annual pasture species. Aust. J. Exp. Agric. and Animal Husbandry. 8:478-483.

Stevens, R., B.C. Giunta, K.R. Jorgensen, and A.P. Plummer. 1977. Winter (Certoides lanata). Utah State Div. of Wildlife Res. Pub. No. 77-2.

Stevens, R., K.R. Jorgensen, J.N. Davis, and S.B. Monsen. 1986. Seed pappus and placement influences on white rubber rabbitbrush establishment. E. Durant McArthur, and Bruce L. Welch (compilers). Proc.--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General technical Rep. INT-200 Ogden, UT: USDA, Forest Serv. Intermountain Forest and Range Exp. Sta.

Stevens, R., and G.A. Van Epps. 1984. Seeding techniques to improve establishment of forage kochia (Kochia prostrata [L.] Schrad.) and fourwing saltbush (Artiplex canescens [Pursh] Nutt.) In: A.R. Tiedemann, E.D. McArthur, H.C. Stutz, R. Stevens and K.L. Johnson (compilers). Proc.--symposium on the biology of Atriplex and related chenopods; 1983 May 2-6; Provo, UT; USDA Forest Serv. General Techical Rep. INT-172. p. 269-272.

Stoddart, Laurence A., and Arthur D. Smith. 1955. Range Manage. 2nd Edition. McGraw-Hill Book Co. New York.

Stolzy, L.J., and K.P. Barley. 1968. Mechanical resistance encountered by roots entering compact soils. Soil Sci. 105:297-301.

Taylor, H.M., and H.R. Gardner. 1960. Use of wax substrates in root penetration studies, Proc. Soil Sci. Soc. Amer. 24:79-81.

Thalen, D.C.P. 1979. Ecology and utilization of desert shrub rangelands in Iraq. Dr. W. Junk B.V., The Hague.

Thornton, N.C. 1945. Importance of oxygen supply on secondary dormancy and its relation to the inhibiting mechanisms regulating dormancy. Contributions From Boyce Thompson Institute. 13:487-500.

U.S. Forest Serv. 1937. Range plant handbook. U.S. Government Printing Office. Washington, D.C.

Vallentine, John F. 1971. Range development
    and improvements. Brigham Young Univ.
    Press. Provo, Utah.

Wasser, C.H. 1945. High protein content makes
    winterfat valuable forage for Colorado
    ranges. Colorado Farm Bull. 7:6-7 and 13.

Wenger, Leon E. 1941. Re-establishing native
    grasses by the hay method. Cir. 208. Agr.
    Exp. Stn., Kansas State College of Agric.
    and Applied Sci. Ft. Hays Branch Station,
    Manhattan, KS.

Wiedemann, H.T., and B.T. Cross. 1981. Rangeland
    seeder development using semicircular seedbox
    and auger agitator seed metering concept.
    J. Range Manage. 34:340-342.

Wiedemann, H.T. 1982. Fluffy grass seed metering
    device for rangeland seeders. p. 178-182. In:
    Earl F. Aldon and Wendall R. Oaks (eds.)
    Proc. 'Reclamation of Mined Lands in the
    Southwest' a symposium, October 20-22.
    Albuquerque, N.M. Soil Conserv. Soc. of
    Amer.

Wood, M. Karl, Richard E. Eckert, Jr., Wilbert
    H. Blackburn, and Fredrick F. Peterson. 1982.
    Influence of crusting soil surfaces on
    emergence and establishment of crested
    wheatgrass, squirreltail, Thurber
    needlegrass, and fourwing saltbush. J.
    Range Manage. 35:282-287.

Woodmansee, R.G., and L.D. Potter. 1971.
    Natural reproduction of winterfat in New
    Mexico. J. Range Manage. 24:24-31.

Young, James A., Raymond A. Evans, Richard O.
    Gifford, and Richard E. Eckert Jr. 1970.
    Germination characteristics of three species
    of Cruciferae. Weed Sci. 18:41-48.

Young, James A., Raymond A. Evans. 1973.
    Mucilaginous seed coats. J. of the Weed
    Sci. Soc. of America. 21:52-54.

Young, James A., Raymond A. Evans, and Burgess
    L. Kay. 1975. Dispersal and germination
    dynamics of broadleaf filaree, Erodium
    botrys (Ca.) Bertol. Agron. J. 67:54-57.

Zemetra, Robert S., Cynthia Havstad, and Robin
    L. Cuany. 1983. Reducing seed dormancy in
    Indian ricegrass (Oryzopsis hymenoides). J.
    Range Manage. 36:239-241.

Zohary, M. 1937. Die verbreitungsokolgischen
    verhaltnisse der pflanzen Palastinas, I.
    Beih Bot. Zentralbl A 56:1-155.

SEEDBED MICROENVIRONMENT, SEEDLING RECRUITMENT, AND PLANT ESTABLISHMENT ON RANGELANDS

Raymond A. Evans and James A. Young[1]

ABSTRACT

Plant establishment by seedling recruitment is only successful when the potential of a species for seed germination and seedling survival is matched with microenvironmental factors of the seedbed. Unfavorable temperature and moisture regimes create harsh conditions for plant establishment. Plant litter cover and a rough microtopography moderate these harsh conditions fostering plant establishment in these seedbeds.

INTRODUCTION

This discussion will have as its basis detailed information about seed germination and establishment of plant species in rangeland seedbeds and the environmental conditions in the high-elevation cold deserts of the Intermountain West, with some reference to the species of the annual grasslands of California. Principles presented will have much broader application than in these two ecosystems.

SEED GERMINATION

Let us now consider germination requirements of a broad spectrum of species in the sagebrush-grass ecosystem, especially those requirements in relation to temperature and available soil water.

Temperature Requirements for Germination

Temperature requirements for germination for the majority of cool-season grasses are similar and fall within a range that occurs normally in the field during the spring or fall in the sagebrush-grass ecosystem (Young and Evans 1982). By evaluating germination responses of the major forage and weedy species occurring or used for revegetation in the sagebrush-grass ecosystem at 55 constant and alternating temperature regimes from 0 to 40 C in the laboratory, Young and Evans were able to compare individual species responses to seedbed temperatures.

Germination of Cool-Season Perennial Grasses

Optimum germination for the majority of cool-season perennial grass species occurred with night temperatures of 10 to 20 C alternating with day temperatures of 20 to 30 C. Some germination occurred at extremes of temperature, but when night temperatures were at 0 C, either constant or alternating with higher day temperatures, germination was extremely slow with low final germination percentage.

Germination of the dominant perennial grasses was reduced at temperatures other than moderate. Germination of the perennial grasses at colder than moderate temperatures averaged 35% of the germination at moderate temperatures; at widely-fluctuating temperatures, 52%; and at warmer than moderate temperatures, 56%. There were some exceptions where germination was only slightly reduced at harsher seedbed temperatures. Maximum germination in the wheatgrasses was only reduced to 88% under widely fluctuating temperature regimes and to 89% in the bluegrasses from that under moderate temperature regimes. Colder than moderate temperatures significantly reduced germination of all perennial grasses from germination with moderate temperatures (Young and Evans 1982).

Germination of Selected Hybrid Grasses

Slightly improved germination of Elytrigia repens (L.) Nevski x Pseudoroegneria spicata (Pursh) Love hybrids under cold and widely fluctuating temperatures compared with that of most adapted and widely used revegetation perennial grasses, crested wheatrass [Agropyron desertorum (Fisch. ex Link) Schult.] and intermediate wheatgrass [Thinopurum intermedium (Host) Barkworth and D.R. Dewey], indicated a potential for selection to overcome adverse temperature regimes in seedbeds (Young et al. 1986). In the future, perhaps, plant breeding and selection can be used for development of better adapted plant material for the harsh seedbed conditions on rangelands.

Dormancy and Germination

Some revegetation species, such as antelope bitterbrush [Purshia tridentata (Pursh) DC.] and cliffrose [Cowania mexicana var. stansburiana (Torr.) Jeps] have afterripening requirements to break seed dormancy that require incubation under specific temperature and moisture regimes to initiate germination (Young and Evans 1981, Evans and Young 1987). When seeds require afterripening not only do temperature-water relations in the seedbed have to be favorable for germination, but also for stratification. Seedbed conditions favorable for stratification for antelope bitterbrush are constant temperature at 0 to 5 C with constant available water for at least 2 weeks. Under field conditions in early spring or late fall, dormancy is usually broken in 3 or 4 weeks (Unpublished data, ARS, Reno, NV). After dormancy is broken, seed germination requires available water and desirable temperatures in the seedbed. The net result of this combination of strict requirements for two necessary processes for germination of seeds is that a longer period of time of available water in the surface soil is required. Therefore only

[1] Range Scientist, retired, and Range Scientist, USDA/ARS, 920 Valley Road, Reno, NV. 89512.

in years of normal or above spring precipitation
is it possible to establish bitterbrush from
seeding on rangeland.

Germination of Weedy Species

The dominant herbaceous weeds on sagebrush
rangelands are better adapted to harsh seedbed
temperature regimes than are perennial grasses
and shrubs. Cheatgrass (Bromus tectorum L.),
tumble mustard (Sisymbrium altissimum L.), and
medusahead [Taeniatherum asperum (Sim.) Nevski]
germinate at a wide range of low and widely
fluctuating seedbed temperatures (Evans and Young
1972). The pioneer weeds Russian thistle
(Salsola australis R. Br.) and barbwire Russian
thistle (Salsola paulsenii Lit.) are particularly
well adapted to harsh seedbed conditions because
they germinate very rapidly and at wide ranges of
temperature. There need not be very long periods
of favorable temperature-moisture conditions for
these weeds to become established (Young and
Evans 1979).

Moisture Requirements for Germination

Adaptation to germinate with varying water
potentials, as with different temperature
regimes, is strikingly different among groups of
plants (Young et al. 1983). With most grasses in
the sagebrush ecosystem, germination decreases
drastically at water potentials lower than 0.8
MPa. With other plants, such as Russian thistle,
germination is not markedly reduced even at 1.6
MPa. On the other hand, antelope bitterbrush
germination is severely reduced at even moderate
water stress levels (0.1 MPa) (Evans and Young
1987).

SEEDBED MICROENVIRONMENTS

Favorable temperatures and available water in
seedbeds for seed germination and plant growth in
the high-elevation cold deserts are inversely
related in their annual cycles. There are
generally two periods of the year, fall and
spring, when favorable temperatures and available
soil water coincide to allow germination and
plant establishment to occur. The coincidence of
occurrence of favorable conditions for plant
establishment from seed varies markedly among
geographical areas in the sagebrush-grass
ecosystem. In the more mesic areas, germination
and establishment in both fall and spring occur
about 80% of the time, while in the more arid
areas of the sagebrush ecosystem, fall
germination only occurs one out of every five
years. Even though there is coincidence of
precipitation and temperature conditions to allow
seedling recruitment, conditions on a bare,
smooth seedbed are harsh and often restricting to
seed germination and seedling establishment.

Favorable Seedbed Microsites

Harper et al. (1965) and Young et al. (1969) have
equated seedling recruitment and plant
establishment to the number of "safe" microsites
provided in seedbeds. The number of safe sites,
not the number of seeds available, determine
population densities. Numerous studies have
shown that safe sites are equated to seed
placement in the soil and the physical
characteristics of the soil surface. The
beneficial effects of plant litter on seedbed
surfaces have been recognized by many authors
(Piemeisel 1951, Heady 1958, Evans and Young
1970). Alteration of the soil surface
topography, either natural or artificial by
furrowing, putting or punching is another
important factor in changing microenvironments of
seedbeds to allow seed germination and seedling
establishment (Harper et al. 1965, McGinnies
1958, and Evans and Young 1972). Soil coverage
of seeds also aids in germination and
establishment.

Plant Litter and Seedling Recruitment

Plant litter is defined as the procumbent stems,
leaves, and inflorescences of plants from the
previous years' growth. In a community dominated
by annual plants or having an annual plant
understory, the standing, dried plants,
especially the grasses, are usually pressed down
by snow following a growing season. Other plants
remain standing, but all contribute to the litter
of a plant community. The effects of plant
litter are most strikingly seen in establishment
of annual weeds because their seeds are generally
dispersed on the surface of the soil and to
maintain themselves requires annual seedling
recruitment. The effects of litter also
constitute a major factor for successful
establishment in aerial seeding of revegetation
species following fire or other disturbance.

The role of plant litter in modifying microsites
in terms of parameters of temperature, available
water in the soil, and moisture in the atmosphere
of the seedbed in an annual rangeland community
was studied by continuous monitoring of these
parameters during seed germination and seedling
establishment (Evans and Young 1970). The effect
of plant litter on seedling recruitment and plant
succession were also investigated.

Temperature and its Modification in the
Seedbed

Both diurnal and seasonal patterns of air
temperature of the seedbed surface were greatly
modified by a cover of plant litter (fig. 1, fig.
2). The result of this modification was to
change temperature regimes on the soil surface
from widely fluctuating, as much as from 5 to
30 C diurnally, to the moderate range (5-15 C)
during periods of seed germination and plant
establishment.

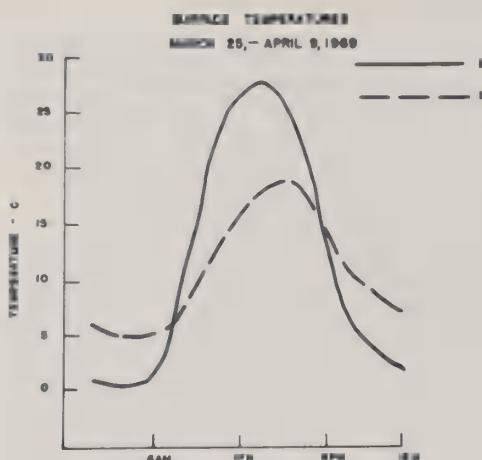SURFACE TEMPERATURES

MARCH 25,– APRIL 9,1969

BARE

LITTER

Figure 1.   Diurnal pattern of air temperature on
the surface of bare soil and that
covered with litter from values taken
by continuous monitoring in the spring
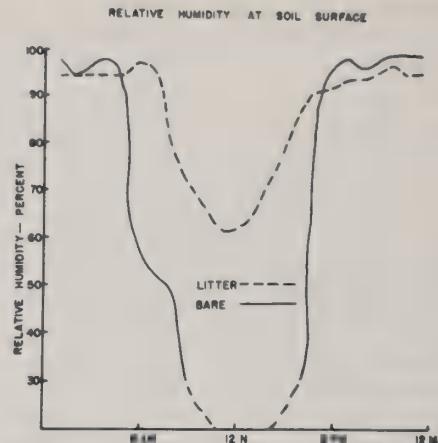growing season of 1969 (Evans and
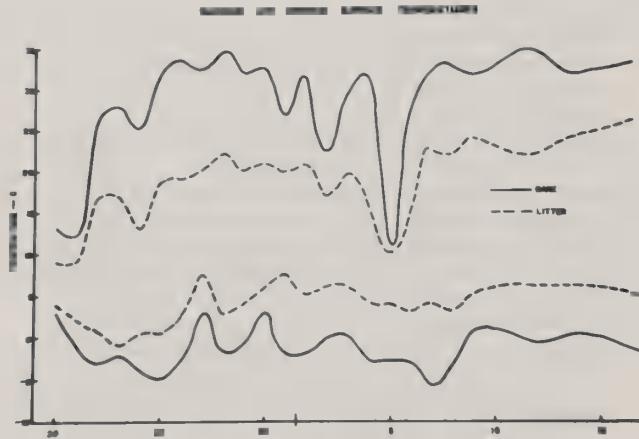Young 1970).

Figure 2.   Maximum and minimum air temperatures on
the surface of bare soil and soil
covered with plant litter during the
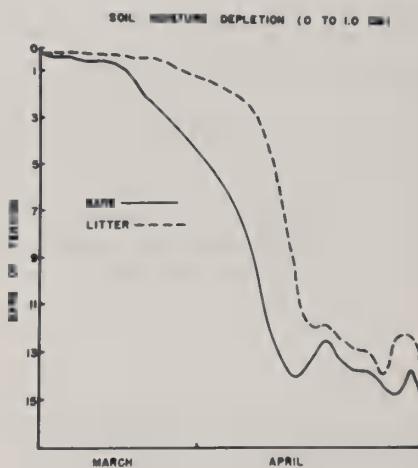spring growing season of 1969 (Evans
and Young 1970).

RELATIVE HUMIDITY AT SOIL SURFACE

LITTER
BARE

Figure 3.   Diurnal pattern of relative humidity
at soil level (0 to 3 cm) for bare
soil and for soil covered with litter
as shown by average values taken in
March and April 1969. Relative
humidity values below 30% are
extrapolated (Evans and Young 1970).

SOIL MOISTURE DEPLETION (0 TO 1.0 cm)

BARE
LITTER

Figure 4.   Soil moisture depletion from the
surface to 1 cm below the surface of
bare soil and that covered with plant
litter during the spring growing
season in 1969 (Evans and Young 1970).

Soil and Atmospheric Water and its
Modification in the Seedbed

Water relations were also dramatically altered.
The diurnal range in relative humidity was
decreased from 98% during early morning and late
afternoon to less than 30% at mid day on bare
soil to 98 to 65% with litter (fig. 3). Plant
litter cover, also, delayed soil moisture
depletion in the surface soil (fig. 4).

General Aspects

In annual plant communities dominated by
cheatgrass or medusahead, litter coverage of the
soil increased seed germination and seedling
establishment of annual grasses, and altered

botanical composition of the stand. Emergence of
medusahead seedlings under litter was 47 times
greater than on bare ground early in the spring
(6200 seedlings compared to 130 per sq m). By
the end of the growing season, medusahead yielded
four times as much under litter as on bare soil.

Litter cover of the seedbed favored seedling
recruitment of cheatgrass in like manner as
medusahead. The interaction between the
germination potential of cheatgrass and tumble
mustard and the changed seedbed conditions caused
by litter cover greatly altered botanical
composition of the stand. Tumble mustard, by
virtue of its small, high density, mucilaginous

214

seeds is able to germinate on bare soil surfaces and dominate under the harsh conditions of bare soil while cheatgrass with a relatively large caryopsis must have the more favorable moisture and temperature conditions that accompany litter coverage. With favorable conditions for germination, cheatgrass outcompetes tumble mustard and other broadleaf plants in the stand. Thus, litter accumulation on the soil surface is the factor driving succession of annuals in the cheatgrass community (Piemeisel 1951).

In broadcast seeding of perennial grasses and other forage plants, success in establishment is dependent on seed coverage by litter, ash, or soil. Similar temperature and moisture conditions prevail with coverage as has been described for annual species.

Soil Microtopography and Seedling Recruitment

A smooth soil surface devoid of litter or other vegetative cover represents the harshest seedbed for seed germination and seedling establishment. Without mollification, either by natural or artificial means, plant establishment by seedling recruitment is almost impossible. Only a few species are adapted for seed germination and seedling establishment under conditions of a bare, smooth seedbed surface. In the previous section, we have seen the effects of accumulated litter on modification of seedbed conditions. We shall now consider the role of microtopography of the soil surface in altering individual microenvironmental parameters to create conditions favorable to seedling recruitment.

In detailed studies, we investigated the role of microtopography of the seedbed in relation to the number of "safe" microsites of the seedbed for annual weedy species on sagebrush rangelands (Evans and Young 1972). We measured parameters of environmental characteristics and related germination and establishment of annual species to individual factors of their environment. Three important and widespread annual weeds were used in these investigations: medusahead, cheatgrass, and tumble mustard. Seeds of each species, at the rate of $5,000/m^2$, were broadcast on the soil surface or buried 1 cm deep; pitting of the soil surface was used to simulate natural seedbed microtopography, pits 3, 6, and 9 cm deep were compared. Studies were conducted in clay and sandy loam soils. These comparisons were made in fall and spring growing seasons. Soil water potentials and air and soil temperatures in the seedbed were continuously monitored during the period of seed germination and seedling establishment. In this manner, seedbed characteristics in terms of individual limiting factors were defined throughout the time of seed germination, seedling growth, and plant establishment.

In the spring study, more than 100 times as many cheatgrass seedlings emerged on clay soil from pits as from smooth soil (6740 versus $67/m^2$, fig. 5). Emergence increased more than 30 times when caryopses were buried 1 cm deep, in comparison to broadcast on the surface of smooth soil (2290 versus $67/m^2$). With tumble mustard, similar results were found, except initial emergence was more rapid and maximum emergence was considerably less (fig. 6). Effects of seedbed differences persisted throughout the growth period and affected herbage production of the two species in like manner. However, by the end of the growing period, cheatgrass had provided severe competition to seedling establishment and growth of tumble mustard.

Results were similar on sandy loam soil (data not presented), but sloughing in of the pits limited emergence and growth by burying seeds and emerging seedlings as much as 7 cm. When seeds of tumble mustard and caryopses of cheatgrass were initially buried in the sandy loam seedbed, the effect of microtopography was negated by the moderating effect of soil coverage on the smooth soil and of soil movement into the pits.

In the fall study, emergence of cheatgrass and medusahead was greatly influenced by microtopographic variation in the seedbed. Three weeks after planting, 30 cheatgrass seedlings were counted on the soil surface, where the caryopses had been unburied, compared with 10,300 seedlings/m^2 in the 9 cm pits. In a similar comparison, there were 40 medusahead seedlings/m^2 on the surface compared with 6010/m^2 in the pits. When caryopses were covered with soil,
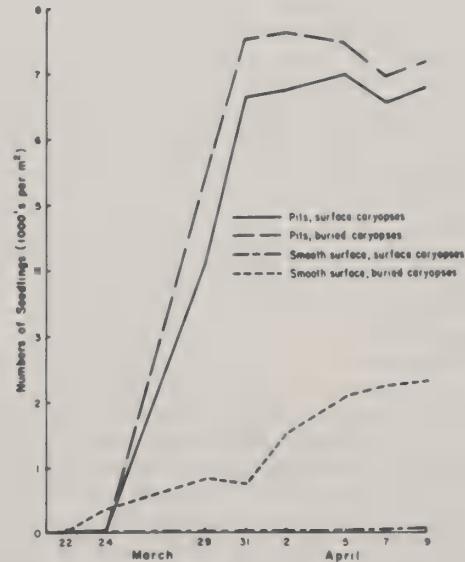

Figure 5. Seedling emergence of cheatgrass during early spring on a clay soil seedbed in relation to microtopography and seed burial (Evans and Young 1972).
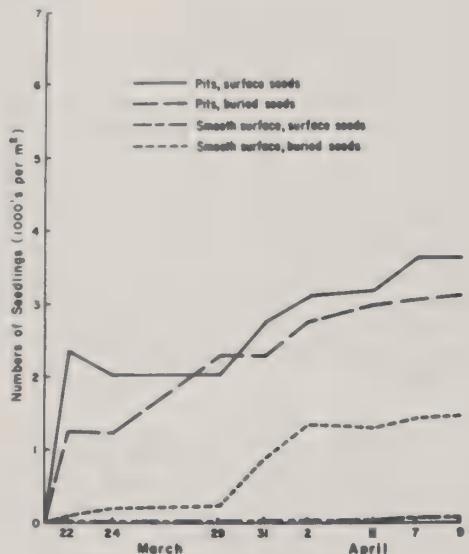
Figure 6. Seedling emergence of tumble mustard during early spring on a clay seedbed in relation to microtopography and seed burial (Evans and Young 1972).

cheatgrass emergence on the surface and in the pits was comparable. Medusahead emergence was greater in the pits than on the surface, even with the seeds covered with soil.

The movement of soil and its subsequent filling in of holes, pits, and crevices materially aids in seed burial, creating a more favorable environment for germination and seedling growth. However, in some cases, soil movement into pits or crevices adversely affected emergence by burying seeds too deeply. Instability and movement of surface soil are directly related to textural differences of soil and to type and amount of precipitaiton during the period of seed germination, seedling emergence, and growth.

About 1% of the grass caryopses and mustard seeds broadcast on the smooth soil surface resulted in seedling establishment in these studies. In contrast, emerging seedlings in pits was over 150% (cheatgrass) or over 100% (medusahead) as great as the number of caryopses seeded. Emergence rate of tumble mustard varied from 20 to 72% in pits. The foregoing indicates, in the case of the two grasses, that the function of microtopography of seedbed surface involves both dispersal and establishment. Because of the small size of the mustard seed, modification of the seedbed on this rather gross scale affected only its establishment. Perhaps on a microscale, as found in nature, dispersal of tumble mustard seeds is also affected by varying micro-topography.

Temperature and its Modification in the Seedbed

Daily maximum temperatures on the soil surfaces varied markedly during the spring period for seed germination and seedling growth, ranging to 40 C commencing the second week after seeding and frequently thereafter (fig. 7). Minimum soil-surface temperatures were 0 to -9 C for the first 4 weeks, except in a rainy period that occurred in the third week. In pits, soil surface temperatures were drastically modified from those on the smooth soil surface. Maximum daily temperatures were as much as 17 C lower in the pits early in the germination period. These temperatures did not exceed 25 C during the first 4 weeks. Minimum soil surface temperatures in the pits were at or above 0 C, except for 4 days when they dipped to a minimum of -3 C. Later in the season, differences in soil surface temperatures on the smooth soil and in pits tended to be less pronounced. At 1 cm below the soil surface, maximum temperatures were 4 ± 2 C lower over the season, minimums were 2 ± 2 C higher in pits than on the soil surface. These modifications were more pronounced early in the season. Similar temperature relations existed with microtopographic differences and soil burial in the different textured soils.

Temperature regimes were relatively constant over the germination period in the fall having temperature ranges of 0 to 20 C at the surface and 5 to 20 C at 1 cm below the soil surface. Modification of temperature regimes by changes in microtopography were slight under these conditions. Degree of temperature modification by differences in microtopography appears to be directly related to the overall soil and air temperature regimes. The effect of soil coverage on temperature is depth related, but is nonlinear (fig. 8).
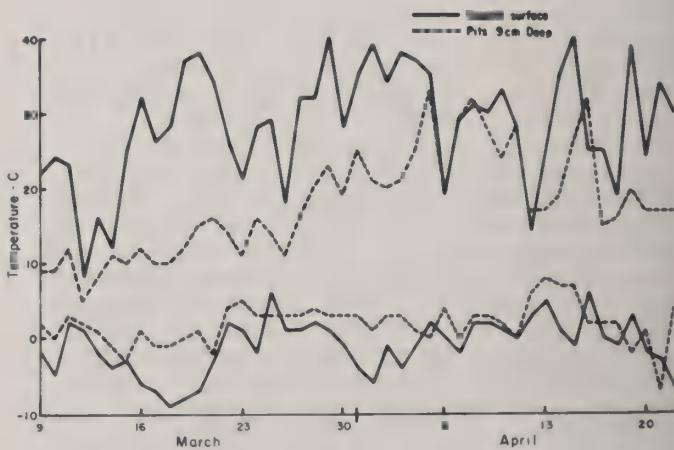

Figure 7. Maximum and minimum air temperatures on the surface of smooth soil in the clay seedbed and of soil at the bottom of 9 cm deep pits during early spring 1971 (Evans and Young 1972).
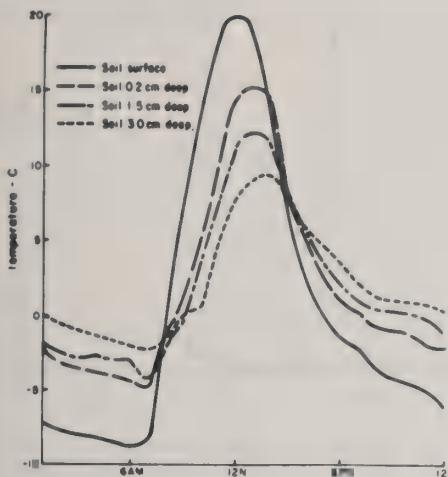
Figure 8. Mean diurnal ranges of temperature in relation to soil depth in a sandy loam soil comparing those from the soil surface to 3 cm deep for 1 week in the fall of 1969 (Evans and Young 1972).

Modification of temperature due to differences in microtopography and soil coverage had a pronounced effect on germination and seedling growth of the three annual species in the study. No germination occurred at subzero night temperatures (-4 and -6 C) alternating with day temperatures from 0 to 30 C. At a 0 C night temperature, germination of mustard and medusahead was greatly depressed by day temperatures greater than 15 C, while cheatgrass germination remains high even at 30 C (Table 1). At 5 C or above night temperatures, optimum germination for all species occurred at day temperature from 5 to 30 C. Seedling growth was minimal for all three species at 0 C night temperature alternating with any day temperature (Table 2). Increased seedling growth was directly related to higher night temperatures (5 C and above), and there was a tendency for growth to decrease when day temperatures exceeded 20 or 25 C.

Soil and Atmospheric Moisture and its Modification in the Seedbed

In the spring on the clay seedbed, soil water potential in the first cm of soil under the smooth soil surface was above -0.2 MPa during the first 3 weeks. During the fourth week, the period of active seedling emergece, soil water potential decreased to -1.5 MPa and below very rapidly. In pits, water potential of the surface soil (0 to 1 cm) remained at a high level (0.03 MPa) throughout the entire season (fig. 9). Similar soil water depletion patterns were found on a sandy loam seedbed. In this instance, a short period of rapid depletion of soil water to 1.5 MPa occurred at the time of initial seedling

emergence on the flat soil surface. Soil water was then depleted in the fourth week as it was in the clay soil. Soil water depletion was nil in the pits during the entire period (fig. 10).

In the fall, soil water at the surface (0 to 1 cm), at maximum depletion, was retained at a lower tension in pits (-0.6 MPa) than on the flat surface (-1.0 MPa). These differences occurred only when most seeds had germinated. Effectiveness of modification of individual environmental parameters depends on overall air and soil temperatures. Timing and amount of precipitation are also important in the effectivensss of these modifications.

Relative humidity of the atmosphere has a direct effect on surface seeds or caryopses, in relation to available water and effective temperature regimes. When water is not available to germinating seeds and growing seedlings on the soil surface, the higher range of temperatures is no longer effective in influencing biologic processes (Evans and Young 1972). Further, water depletion of the surface soil is influenced by a rapidly drying soil-air interface, even at low temperatures under a high stress atmosphere.

General Aspects

Results of these study indicate that depressions on the soil surface (rough versus smooth microtopography) increase germination of seeds and establishment of seedlings by altering their physical environment. The depressed sites retain soil water at the surface longer and have more favorable atmospheric moisture and temperature regimes than a flat surface. Also, a rough seedbed encourages more adequate soil coverage of the seeds, which in turn, further modifies the microenvironment. Relative effectiveness of seedbed modifications, resulting from rough microtopography or litter cover, is dependent on timing of germination and seedling growth in relation to temperature and water regimes. In moist, warm periods, germination and growth can occur irrespective of these modifications. However, usual rangeland conditions are harsher and favorable microtopography or litter cover is necessary for establishment of annual species.

SYNTHESIS

Plant establishment by seedling recruitment is successful only when factors of the microenvironment are matched to the potential of a species for seed germination, seedling emergence, and subsequent growth. In many rangeland environments conditions of the seedbed are too harsh for successful establishment of plants without placing seeds in the most favorable microsites or artificially modifying characteristics of the seedbed.
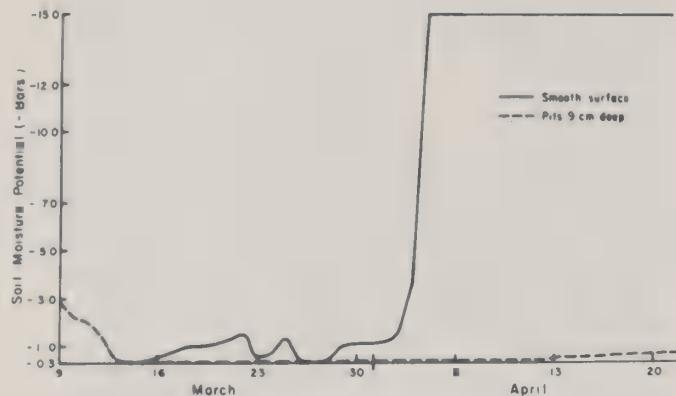
Figure 9. Soil-water potential in relation to microtopography of a clay-soil seedbed in spring 1971 (Evans and Young 1972).
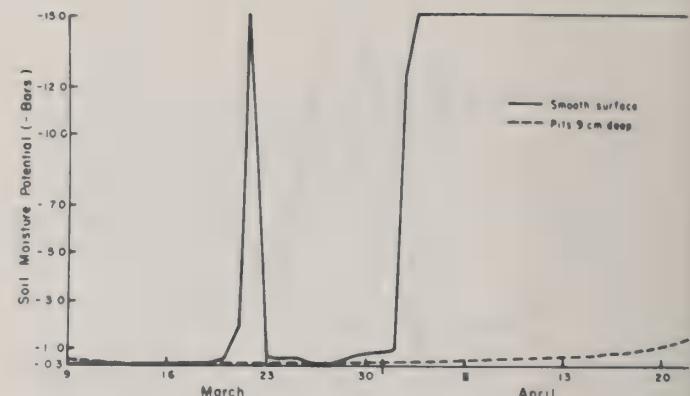

Figure 10. Soil-water potential in relation to microtopography of a sandy loam seedbed in spring 1971 (Evans and Young 1972).

Table 1. Germination of cheatgrass, medusahead, and tumble mustard after 2 weeks incubation under alternating day (8 hr) and night (16 hr) temperatures (Evans and Young 1972).

Night temperatures (16 hr)	Day temperatures (8 hr)							
	0	2	5	10	15	20	25	30
Cheatgrass	----------------------------- Germination percentage -----------------------------							
0.........	0 a	54 b	87 cd	97 cd	88 d	91 d	82 cd	71 c
2.........		76 c	81 cd	84 cd	80 cd	79 cd	72 c	80 cd
5.........			100 d	97 d	97 d	96 d	80 cd	79 cd
10.........				98 d	100 d	96 d	94 d	90 d
15.........					100 d	100 d	96 d	94 d
20.........						99 d	96 d	99 d
25.........							98 d	91 d
30.........								52 b
Medusahead								
0.........	0 a	56 bc	76 d	52 c	76 d	8 a	12 a	0 a
2.........		76 d	80 de	92 de	96 de	60 bc	0 a	0 a
5.........			96 de	92 de	92 de	96 de	60 bc	28 b
10.........				96 de	100 e	92 de	92 de	92 de
15.........					100 e	100 e	92 de	92 de
20.........						96 de	92 de	92 de
25.........							52 c	76 d
30.........								36 bc
Tumble mustard								
0.........	0 a	32 b	52 bc	88 cd	80 cd	20 ab	0 a	0 a
2.........		28 ab	40 bc	76 cd	76 cd	72 cd	84 cd	0 a
5.........			76 cd	80 cd	92 cd	96 cd	92 cd	68 c
10.........				100 d	92 cd	96 cd	92 cd	88 cd
15.........					92 cd	100 d	88 cd	96 cd
20.........						92 cd	92 cd	96 cd
25.........							96 cd	84 cd
30.........								76 cd

Table 2. Seedling length of cheatgrass, medusahead, and tumble mustard after 2 weeks incubation under alternating day (8 hr) and night (16 hr) temperatures (Evans and Young 1972).

Night temperatures (16 hr)	Day temperatures (8 hr)							
	0	2	5	10	15	20	25	30
Cheatgrass	------------------------------ Seedling length (mm) ------------------------------							
0........	0 a	2 b	2 a	2 a	2 a	4 ab	4 ab	4 ab
2........		2 a	2 a	3 ab	8 ab	8 ab	10 ab	13 b
5........			16 b	23 b	38 c	38 c	40 c	52 d
10........				55 d	80 f	68 e	80 f	78 ef
15........					85 fg	82 f	93 g	80 f
20........						116 h	90 fg	90 fg
25........							120 h	90 fg
30........								70 ef
Medusahead								
0........	0 a	3 ab	3 ab	2 ab	5 ab	0 a	0 a	0 a
2........		5 ab	4 ab	14 ab	21 b	24 b	1 a	0 a
5........			11 ab	17 ab	31 b	37 b	25 b	21 b
10........				70 cd	84 d	105 e	74 cd	59 c
15........					126 f	113 ef	128 fg	106 e
20........						146 g	130 fg	106 e
25........							142 fg	104 e
Tumble mustard								
0.........	0 a	2 a	2 a	3 a	3 a	3 a	3 a	1 a
2.........		2 a	3 a	10 b	10 b	9 ab	11 b	0 a
5.........			3 a	5 ab	10 b	15 bc	18 cd	24 de
10.........				4 a	6 ab	32 ef	27 de	23 d
15.........					37 f	32 ef	29 e	23 d
20.........						29 e	30 e	29 e
25.........							16 c	9 ab
30.........								11 b

The foregoing discussion has centered on seedling recruitment of annual species in relation to seedbed characteristics, but the same principles apply with perennial, revegetation species. Safesites, sites in the seedbed that will allow seed germination and plant establishment, for a particular species will determine successful recruitment of that species. These safesites have been characterized in terms of individual parameters of the microenvironment and factors limiting germination and growth have been defined.

In the cold deserts of the Intermountain West, in particular the sagebrush ecosystem, limiting factors for natural seedling recruitment and successful seeding of revegetation species are available soil water, favorable temperature regimes, and atmospheric moisture in and on the seedbed. Many studies have shown that proper seedbed preparation is essential for successful seeding. McGinnies (1958) related furrowing to moisture content of the soil and subsequent seedling establishment. In a microenvironmental monitoring study, Evans et al. (1970) showed that furrowing mollified the microenvironment for seeds and seedlings by changing temperature and water regimes to create safesites for successful seeding. Their research also emphasized and characterized the effects of weed competition as a limiting factor in the seedbed. The limiting factor associated with competition was found to be lack of available soil water for plant survival and growth.

Development of the deep furrow drill arm assembly for the rangeland drill was predicated on the safesite concept in seedbeds and its use was shown to enhance seeding success (Asher and Eckert 1973). The atrazine-fallow method for control of cheatgrass (Eckert and Evans 1967) was based on the concept and owes its success to the principle of creating an unfavorable seedbed for cheatgrass and subsequently altering the seedbed to allow successful seeding of perennial grasses.

In the annual rangelands of California, seedbed factors limiting establishment of perennial grasses and annual clovers are far different from those that limit establishment of replacement species in the sagebrush ecosystem. During the period of seed germination and seedling growth (early fall and the beginning of the rainy season), water is normally not limiting and temperatures are favorable for these activities. The limiting factor for seedling establishment on California annual ranges was found to be shading of emerging seedlings of the replacement species by adjacent annual plants (Evans et al. 1975). Again, on California annual rangelands, as was true in the sagebrush ecosystem, safesite definitions and requirements differ with individual species. The effects of shade competition on perlagrass (Phalaris tuberosa var. hirtiglumis Batt. and Trabut.) drastically limited its establishment, while that of the annual clovers (Trifolium spp.) was only marginally affected.

LITERATURE CITED

Asher, J.E. and R.E. Eckert, Jr. 1973. Development, testing, and evaluation of the deep furrow drill arm assembly for the rangeland drill. J. Range Manage. 26:377-379.

Eckert, R.E., Jr. and R.A. Evans. 1967. A chemical fallow technique for control of downy brome and establishment of perennial grasses on rangeland. J. Range Manage. 20:35-41.

Evans, R.A., H.R. Holbo, R.E. Eckert, Jr., and J.A. Young. 1970. Functional environment of downy brome communities in relation to weed control and revegetation. Weed Sci. 18:154-162.

Evans, R.A., B.L. Kay, and J.A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. Hilgardia 43:79-102.

Evans, R.A. and J.A. Young. 1970. Plant litter and establishment of alien weed species in rangeland communities. Weed Sci. 18:697-703.

Evans, R.A. and J.A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. Weed Sci. 20:350-356.

Evans, R.A. and J.A. Young. 1987. Seed germination and seedling establishment of antelope bitterbrish. Proceedings Soc. for Range Manage. 40th Annual Meeting (In Press).

Harper, J.L., L.T. Williams, and G.R. Sagar. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants. J. Ecology 539:273-286.

Heady, H.F. 1958. Vegetational changes in the California annual type. Ecology 39:402-416.

McGinnies, William J. 1958. The relationship of furrow depth to moisture content of soil and to seedling establishment on a range soil. Agronomy J.

Piemeisel, R.L. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology 32:53-72.

Young, J.A. and R.A. Evans. 1979. Barbwire Russian thistle seed germination. J. Range Manage. 32:322-336.

Young, J.A. and R.A. Evans. 1981. Germination of seeds of antelope bitterbrush, desert bitterbrush, and cliff rose. U.S. Dept. of Agriculture, Science and Education Administration, Agricultural Research Results, ARR-W-17. 39 p.

Young, J.A. and R.A. Evans. 1982. Temperature profiles for germination of cool season range grasses. U.S. Dept. of Agriculture. Agricultural Research Service. Agricultural Research Results, ARR-W-27. 91 p.

Young, J.A., R.A. Evans, and R.E. Eckert, Jr. 1969. Population dynamics of downy brome. Weed Sci. 17:20-26.

Young, J.A., R.A. Evans, B.A. Roundy, and G. Cluff. 1983. Moisture stress and seed germination. U.S. Dept. of Agriculture, Agricultural Research Service. Agricultural Reviews and Manuals. ARM-W-36. 41 p.

Young, J.A., R.A. Evans, D.A. Johnson, and K.H. Assay. 1986. Cold-temperature germination of Elytrigia repens x Pseudoroegneria spicata hybrids. J. Range Manage. 39:300-302.

MODIFICATIONS OF SEEDBEDS WITH NATURAL
AND ARTIFICIAL MULCHES

Burgess L. Kay

ABSTRACT

Soil may be the only cost effective mulch for
range seedlings. Effective mulches for land
reclamation are straw or hay, fibers and
chemicals used in hydraulic seeding, and fabrics
stapled to the surface. Most mulches encourage
plant establishment as well as absorb the impact
of raindrops and trap soil particles until
vegetation becomes established.

INTRODUCTION

Mulching to modify the environment of the
germinating seed is one of the few options
available to improve the success of wildland
seeding. Although adding mulch materials is
generally too expensive to consider in rangeland
seeding, the cost can be justified following
mining or other high-value disturbance.

Soil manipulations are a mulching practice which
is cost effective for range seeding. Examples
are the use of soil for seed coverage, soil
firming, deep furrowing, and pitting. Soil to
be used as a mulch is already on the site and
needs only to be manipulated. Such seedbed
modifications and planting techniques are the
subject of many of the papers presented at this
conference. They are presented as ways to modify
the seedbed ecology to improve seedling
establishment which is one of the main functions
of mulching. Mulches may modify the extremes of
temperature and moisture by shading and
encouraging infiltration and water retention.

Also important if the mulch is to be used on
slopes is the protection of the soil surface from
the impact of raindrops and trapping of soil.
Effective mulches will prevent soil being
dislodged by raindrops and subsequently washed or
blown away before the vegetation is sufficiently
established to protect and bind the soil.

METHODS AND MATERIALS

Soil protection was measured by applying the
mulch materials to a variety of soil surfaces
(0.6 x 1.2m) inclined at 5:1 and 2:1 (horizontal
to vertical measurement) and subjecting them to
artificial rainfall (3 mm diameter raindrops
falling a distance of 4.6 m at the rate of 15
cm/hr). Soil in the runoff water was collected
and measured.

[1] Wildland Seeding Specialist, Dept. of
Agronomy and Range Science, University
of California, Davis, CA 95616.

Plant responses were observed on similar surfaces
and also on field applications at Lake Tahoe
(elevation 1,800 m and decomposed granite soil)
and near Davis, California (elev. 15 m and clay
soil).

Mulches tested include straw (barley straw at
1,120 to 8,960 kg/ha) hydraulic fibers (aspen
fiber at 1,680 and 3,360 kg/ha) fabrics (jute,
excelsior, and strips of paper in synthetic
yarn (Hold/grow)) and gums and glues commonly
used in hydraulic seeding.

RESULTS

Soil protection

Straw is very effective at protecting the
surface of the soil from raindrop impact and
also retains significant amounts of soil.
Increasing the rate of straw increases the
effectiveness (fig. 1). Rates from 1,120 to
3,360kg/ha were surface applied and held down
with a tackifier (sticky substance' such as
asphalt emulsion), while the 8,960 kg/ha rate
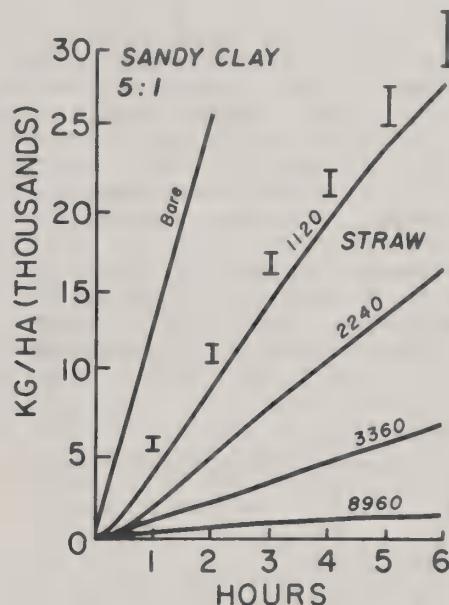was punched into the soil in a split
application (Kay, 1983).

Figure 1. Effect of straw mulch rates on (kg/ha)
soil loss on 5:1 slopes, sandy clay
loam soil. Vertical insets indicate a
significant difference at .05 level.

Hydraulic mulches are similar in cost to straw
applications, but are much less effective in
retaining soil (fig. 2). The particle sizes are
too small to effectively absorb the impact of
raindrops or trap soil particles. They can be
applied to steeper slopes than straw or fabrics
and can be applied in a single application with
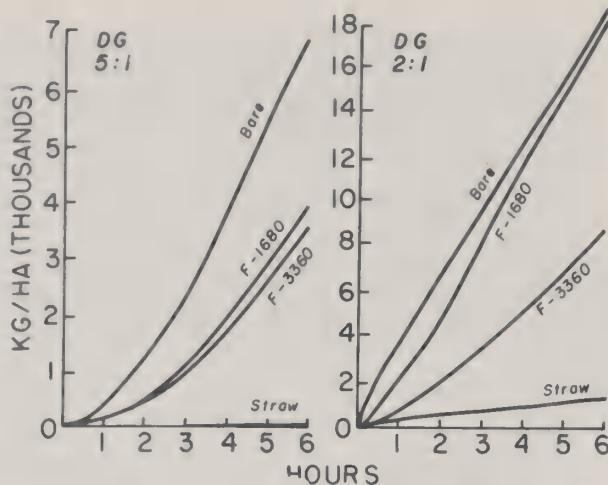seed, fertilizer, and a variety of additives.

Figure 2. Effects of mulch treatments on soil loss (hydraulically applied wood fiber at 1,680 and 3,360 kg/ha and straw at 3,360 kg/ha compared to bare soil) on decomposed granite slopes at 5:1 and 2:1. slopes.

Gums and glues are sometimes added to hydraulic applications to bind mulches and/or soil particles. Effectiveness and cost varies greatly with the type of product, site condition, dilution rate, and split vs. single application (Kay, 1978a, 1978b). Most effective are "white glue" types (polyvinyl acetates (PVA), copolymers of methacrylates and acrylates, and styrene butadiene (SBR)). Less effective are products made from natural plant products such as *Plantago insularis* Eastw., seaweed, or guar (*Cyamopsis tetragonolobus* (L.) Taub.) or starch-graft-polymers (super slurper). Fertilizers may or may not be compatible with these products.

Split applications, applying the seed and fertilizer in the first application and the glue and at least part of the fiber in a second application can increase the effectiveness (fig. 3).

Dilution rate can also be important (fig. 4). Glue products are often improperly applied by using too much water. Hydroseeders apply only 3.5-5% solids by weight. Thus a lot of water is required to successfully apply the fiber. Often too much water is used and the product, though very expensive, is ineffective.
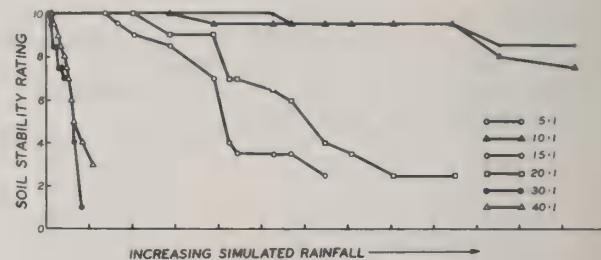
Figure 4. Effect of simulated rainfall on the surface stability of sand treated with 1,120 kg/ha PVA solids at various dilution rates. 10 equals very stable, 1 is unstable.

Fabrics can be effective if properly applied, but are expensive because of the high material cost and labor required to install them. The best fabrics compare in effectiveness to straw (fig. 5) and their performance can be improved even on very steep slopes by application over a layer of straw (fig. 6).

Figure 3. Effect of increasing rainfall on surfaces treated with SBR at 187 ℓ/ha, comparing single and split applications. 10 equals very stable, 1 is unstable.
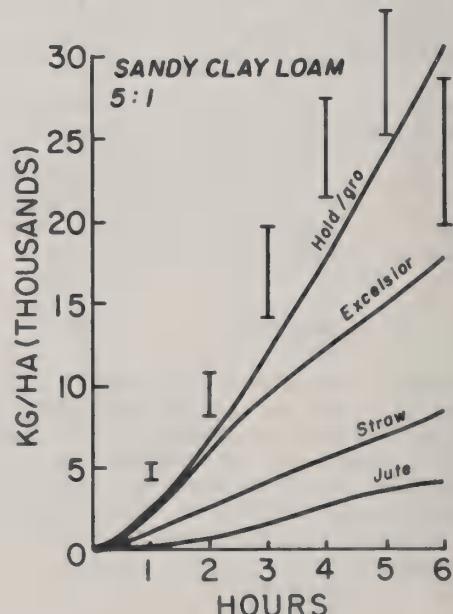
Figure 5. Effect of erosion control fabrics and straw (3,360 kg/ha) on soil loss on 5:1 slopes, sandy clay loam soil. Vertical insets indicate significant difference at .05 level.
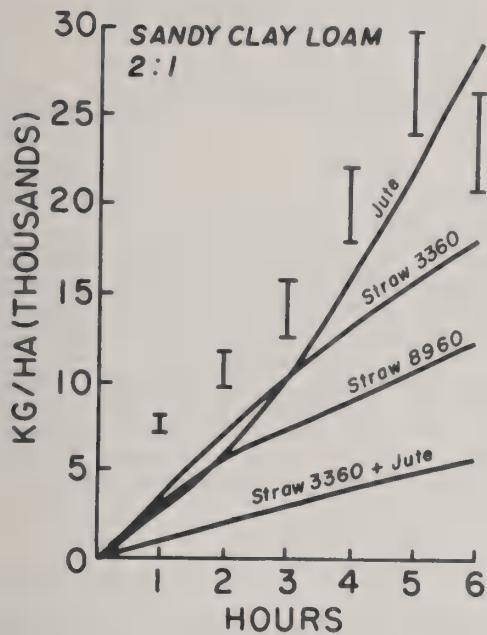
Figure 6. Effect of erosion fabrics or straw broadcast at 3,360 kg/ha or punched into the soil at 8,960 kg/ha on soil loss on 2:1 slopes, sandy clay loam soil. Vertical insets indicate significant difference at .05 level.

Effects on plant establishment

Straw consistently benefits plant establishment compared to no mulch or wood fiber in controlled studies on container grown experiments (Table 1). Similarly in field studies at Lake Tahoe straw was successfully used to effect plant establishment after all other treatments had failed.

Hydraulic seedings/mulchings are successful only in climates with favorable rainfall distribution or if irrigated. The seed is confined to the soil surface by the mulch and has little chance to grow if minimal rainfall conditions persist. Success is improved by increasing the rate of

fiber mulch with rates as high as 5,040 kg/ha showing improved stands. However, economics and the physical limitations of keeping such a "wet rug" on the slope generally limit applications to 1120-2240 kg/ha. A mulch effect (modifying seedling environment) begins at about 1680-2240 kg/ha. Part of the success of hydraulic seeding is the use of high seeding rates, with a minimum of 58 kg/ha being common.

Chemicals to be added to hydraulic seeding are advertised to improve plant establishment and growth. I found chemicals cannot be depended on to do this, and may actually decrease plant establishment by depriving the seed of moisture or increasing moisture and allowing seed germination before there is sufficient moisture present to permit plant growth.

Fabrics are usually heavy enough to modify the seedling environment and improve stands. However, some lightweight products may not contribute a mulch effect, and may flap in the wind, removing the seed. Straw placed beneath the fabric would likely improve seeding success.

DISCUSSION

Mulching practices vary considerably in cost and effectiveness. Characteristics of the site to be stabilized may determine the only practical treatment. However, there are usually alternative methods which should be considered.

Seed coverage and type and amount of mulch should be the first consideration. Seed germination and plant establishment will be improved more by seed coverage with soil than by any other treatment. Mulch treatments generally increase in effectiveness with both the amount of mulch per acre and the length of the fiber. While it is possible to apply excessive amounts of mulch, economic considerations usually prevent it. The importance of fiber length, however, should not be overlooked. Increasing the fiber length (as from wood cellulose fiber to straw) may greatly increase the effectiveness of erosion control and

Table 1. Effect of hydromulch fiber rate or straw on emergence of blando brome (Bromus mollis) on different soils and slope gradients.

Treatment	Approx. kg/ha	No. seedlings/0.09 m^2					
		Decomposed granite				Clay loam	Fine sand
		2:1	1.5:1	1:1	1:1	1:1	1:1
None		7	1	0	0	0	0
Wood fiber	1,120	6	13	10	0	86	0
Wood fiber	2,240	26	29	27	14	262	3
Wood fiber	3,360	35	35	20	58	300	16
Straw + tackifier	2,240	119	131	155			
LSD 0.05		11	8	8	11	68	10

germination (Kill et al., 1971; Perry et al., 1975). This relatively large increase in effectiveness can be achieved at little or no increase in cost.

The most expensive practice is not necessarily the most effective. For example, straw plus a tackifier is more effective for both erosion control and plant establishment than many of the more expensive treatments. A rough seedbed or covering the seed may be the cheapest and most effective treatment for establishing vegetation.

LITERATURE CITED

Kay, Burgess L. 1978a. Mulch and chemical stabilizers for land reclamation in dry regions. pp. 467-483 in Stelly, M. Reclamation of drastically disturbed lands. Amer. Soc. Agronomy, 742 p.

Kay, Burgess L. 1978b. Mulches for erosion control and plant establishment on disturbed sites. Agronomy Progress Report 87, U.C. Davis. 19 p.

Kay, Burgess L. 1983. Straw as an erosion control mulch. Agronomy Progress Report 140, U.C. Davis. 11 p.

Kill, K. D. and L. E. Foote. 1971. Comparisons of long and short-fibered mulches. Trans. ASAE pp. 942-944.

Perry, H. Douglas, D. L. Wright, and R. E. Blaser. 1975. Producing vegetation on highway slopes concurrently with and subsequent to highway construction. Final Report-Proj. 40. West Virginia Dept. of Highways.

EFFECTS OF CLIMATE AND SOILS ON THE DISTRIBUTION OF FOUR AFRICAN GRASSES

J.R. COX[1], M.H. MARTIN-R.[2], F.A. IBARRA-F.[2],
J.H. FOURIE[3], N.F.G. RETHMAN[4], AND D.G. WILCOX[5]

ABSTRACT

Grasslands in the northern and southern
hemispheres have and continue to be invaded by
woody shrubs, and attempts to reestablish
perennial grasses from seed have been on going
for 100 years. Buffelgrass (Cenchrus ciliaris),
weeping lovegrass (Eragrostis curvula),
kleingrass (Panicum coloratum), and Lehmann
lovegrass (Eragrostis lehmanniana) are the most
successfully established and long-lived. The
effects of temperature, precipitation, and soil
type on plant establishment and persistence are
discussed.

INTRODUCTION

Commercial and religious rivalries among the
Dutch, English, Portuguese, and Spanish between
1450 and 1550 resulted in the establishment of
shipping lanes and exploration of continental
land boundaries. Coastal exploration was
followed by colonization, and by 1900 European
settlers and their livestock had occupied the
seemingly endless temperate and semiarid
grasslands of Africa, Australia, North America
and South America. As European man and domestic
livestock numbers increased there was a
corresponding increase in weed and woody shrub
densities, and grassland productivity declined
(Sellers and Hill 1974, Cooke and Reeves 1976).

Between 1880 and 1930, frequent droughts
occurred in Africa, Australia, and North
America, and livestock numbers declined (Brooks
1929, Bogdan 1961, Cox et al. 1983a). In an
attempt to stabilize livestock populations,
botanists, ranchers, and military personnel from
Australia, England, South Africa, and the United
States travelled throughout the world searching
for a "miracle plant" that could produce an
abundance of good quality forage with limited
precipitation. Attempts were also made to
develop high producing varieties through plant
breeding that would surpass native species
(Thornber 1905). Their approach was to: (1)
collect seed from plants growing in harsh

environments, (2) plant seed at experimental
stations or ranches in their respective
countries, (3) increase seed from species that
appeared to be drought tolerant, and (4) plant
seed under extreme climatic and edaphic
conditions (Griffith 1901). From thousands of
seeding trails conducted throughout the world,
four warm-season African grasses were recognized
for their ease of establishment, persistence and
forage production. The grasses were buffelgrass
(Cenchrus ciliaris), weeping lovegrass
(Eragrostis curvula), kleingrass (Panicum
coloratum), and Lehmann lovegrass (Eragrostis
lehmanniana). The purpose of this paper is:

1. To determine where the original seed sources
were collected, and by whom,

2. To determine where the four grasses have
been successfully established from sown seed,
where mature plants have persisted for more than
20 years, and where seed from mature plants has
colonized new areas,

3. To discuss relationships between climate,
soils and pests which may influence the long-
term persistence of the four grasses and,

4. To evaluate the results as they may apply to
future seedings throughout the northern and
southern hemispheres.

MATERIALS AND METHODS

Historical records and journals were examined to
determine (1) where seed were originally
collected and (2) countries where each grass had
been successfully established. Rangeland
conservationists in each country provided
estimations of the area sown to each grass as
well as adjacent colonized areas.

Climatic and edaphic data were collected at or
from nearby areas where seed were originally
collected and where mature plants established
from seed persisted for 20 or more years.
Climatic reporting stations were selected based
upon (1) topographic similarities between
reporting stations and the area where seed were
collected or established, and (2) having 10 or
more years of continuous records which
corresponded with actual planting or invasion
years.

Climatic data are summarized in the following
mean monthly categories: (1) maximum
temperatures, (2) minimum temperatures, and (3)
precipitation. Data from stations in the
northern and southern hemispheres are adjusted
by month so that spring, summer, and fall
seasons correspond.

RESULTS AND DISCUSSION

Initial plant establishment from seed was
documented in 31 countries for buffelgrass, 15
for weeping lovegrass, 9 for kleingrass, and 5
for Lehmann lovegrass. Long-term persistence
and colonization, however, occurred only in 6
countries for buffelgrass, 3 for weeping
lovegrass, 2 for kleingrass and 1 for Lehmann
lovegrass.

[1]Range Scientist, USDA-ARS, Aridland Watershed
Management Research Unit, 2000 E. Allen Road,
Tucson, Arizona 85719, U.S.A.
[2]Head of Department Range Management and
Technical Director, respectively, CIPES,
Hermosillo, Mexico.
[3]Manager, Sentraalwes Agricultural Center,
Bloemfontein, South Africa.
[4]Professor, Department of Plant Production,
University of Pretoria, Pretoria, South Africa.
[5]Principal Advisor, Department of Agriculture
(retired), South Perth, Western Australia.

Buffelgrass

C.J.J. van Rensburg, Department of Agriculture, Union of South Africa, collected buffelgrass seed at many semiarid northeast African locations between 1940 and 1945. Seed were sown at Rietvlei Plant Introduction Station near Pretoria and evaluated for establishment, persistence and forage production. Plants from seed collected in the Turkana Desert of northcentral Kenya and southern Ethiopia in 1940 survived a drought in 1942, and a seed production program was initiated in 1945.

Seed were sown on approximately 500,000 ha of degraded rangeland in southern Africa between 1945 and 1965. It is not possible, however, to attribute all successful plantings in this area to sown seed, because naturally occurring buffelgrass stands were present.

Seed from the Turkana Desert collection were shipped to the United States in 1946, and numbered 153671 (Holt 1985). Plants were successfully established and persisted in southern Texas, and the U.S. Department of Agriculture, Soil Conservation Service informally released T-4464 buffelgrass in 1949. Between 1949 and 1985, Texas seed producers sold 7 million kg of T-4464 seed, and ranchers in southern Texas established the grass on over 4 million ha. Seed were transported south into Mexico and successfully established on 6 million ha along the eastern coast, and on 600,000 ha along the western coast. T-4464 as well as seed from other buffelgrass collections made in Pakistan and southern Africa (Ivory et al. 1974) were shipped to Australia and successfully established on 7.5 million ha in the western and northern territories (Humphreys 1967).

Various buffelgrass accessions have been selected for production and cold tolerance (Das et al. 1978, Ivory and Whiteman 1978, Khan and Zarif 1982). Neither factor, however, can be repeatedly shown to differ among accessions when tests were conducted under the same or similar climatic and edaphic conditions.

Where buffelgrass occurs in northcentral Kenya and southern Ethiopia elevations vary from 150 to 700 m, and mean monthly minimum and maximum temperatures annually vary from 21 to 24°C and 31 to 36°C (Fig. 1), respectively. Rainfall is bimodally distributed in two summer growing seasons, and annually varies from 200 to 400 mm. Buffelgrass is generally found growing in loam and sandy clay loam soils, and growth occurs whenever soil moisture is available (National Animal Husbandry Research Station Annual Report from Naivasha, Kenya 1979).

Where buffelgrass has been successfully established from seed elevations vary from 6 to 830 m, but mean minimum winter temperatures at these locations are 10 to 15°C colder than in the Turkana Desert (Fig.1). Leaf growth begins when mean minimum temperatures rise above 10°C, but active growth occurs only during summer when mean minimum temperatures are between 15 and 20°C and mean maximum temperatures are below 40°C in southern Africa (du Toit el al. 1973, Dye and Walker 1980), northeastern and

northwestern Australia (Humphreys 1967, Sweeney and Hopkinson 1975, Harsh et al. 1981), eastern and western Mexico (Cota and Johnson 1975, Molina el al. 1976), and the southcentral United States (Hanselka 1985). Annual rainfall varies from 200 mm in the Turkana Desert and northwestern Mexico to 1250 mm in northeastern Australia, and may be distributed in either a summer peak, bimodally in summer, bimodally in summer and fall or bimodally in summer and winter.

Buffelgrass seed, from plants established on planted sites, actively colonize adjacent non-planted sites in Kenya, southern Africa, northwestern Australia and northwestern Mexico. At all locations, summer rainfall during active plant growth varies from 170 to 400 mm while rainfall during dormancy varies from 10 to 285 mm (Fig. 2), dry periods totalling 150 to 210 days occur in either winter or in fall and spring, and mean minimum temperatures in the coldest month range between 0 and 23°C. Under such conditions, buffelgrass seed in soil may remain viable for 3 years (Winkworth 1963).

Established stands persist but do not actively colonize adjacent non-planted sites in northeastern Australia, southwestern Mexico, eastern Mexico and southern Texas. Summer rainfall exceeds 440 mm in northeastern Australia and southwestern Mexico, while rainfall during dormancy generally exceeds 300 mm in northeastern Australia, eastern Mexico and southern Texas (Fig. 2). Plant distribution under these environmental conditions is limited by allelopathy (Hussain and Ilahi 1982), competition with more productive forbs and grasses (Sweeney and Hopkinson 1975), insects which reduce plant vigor (Reis et al. 1984), and pathogens (Azmi and Singh 1985) which reduce seed germination during extended wet periods in either summer or winter.

In southcentral Texas, mean minimum temperatures in the coldest month are below 6°C, rainfall during dormancy generally exceeds 400 mm (Fig.3), and an extended dry period does not occur. Stands established harshed under these conditions fail to persist because seed produced in summer is destroyed during wet winters (Amzi and Singh 1985) and established plants die during cold winters (Holt 1985).

Weeping Lovegrass

L.W. Kephart and R.L. Piemeisel, Bureau of Plant Industry, U.S. Department of Agriculture, collected weeping lovegrass seed in northcentral Tanzania in 1927 (Crider 1945). Seed were collected from plants growing in black, waxy, sun-cracked soil on an escarpment between Mbula and Ngorongoro Craters, where elevation varied from 1,300 to 1,800 m.

Seed were shipped to Arizona, United States, in 1932 and numbered A-67 (Crider 1945). Weeping lovegrass was initially thought to be adapted in the semiarid southwestern United States, but mature plants were unable to survive spring and summer droughts (Bridges 1941, Judd and Judd 1976). Mature plants from seed planted in
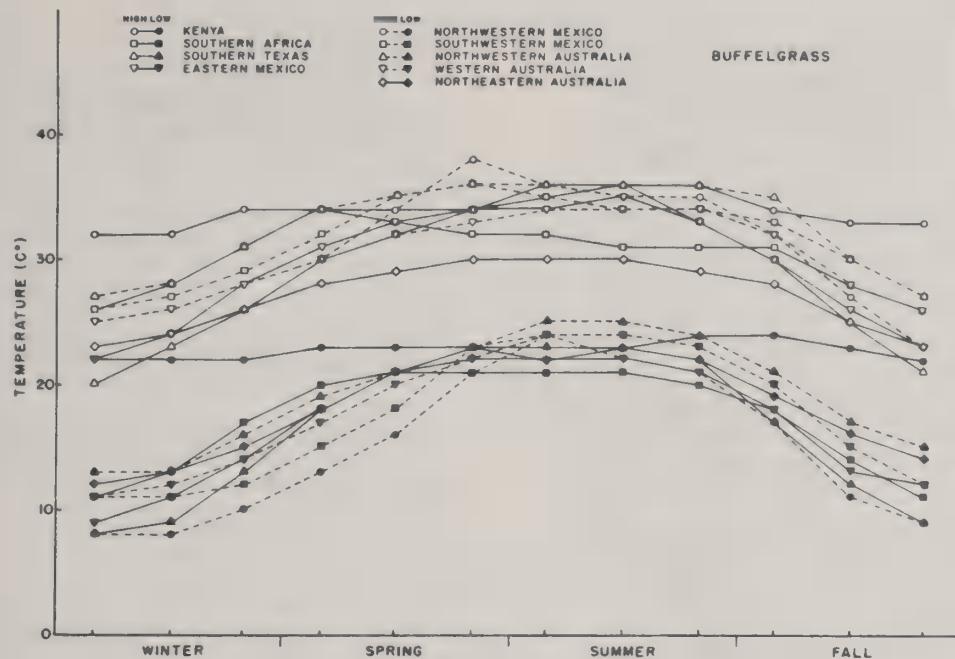
Figure 1. Mean monthly maximum and minimum temperatures during winter, spring, summer, and fall where buffelgrass has been successfully established in the northern and southern hemispheres.
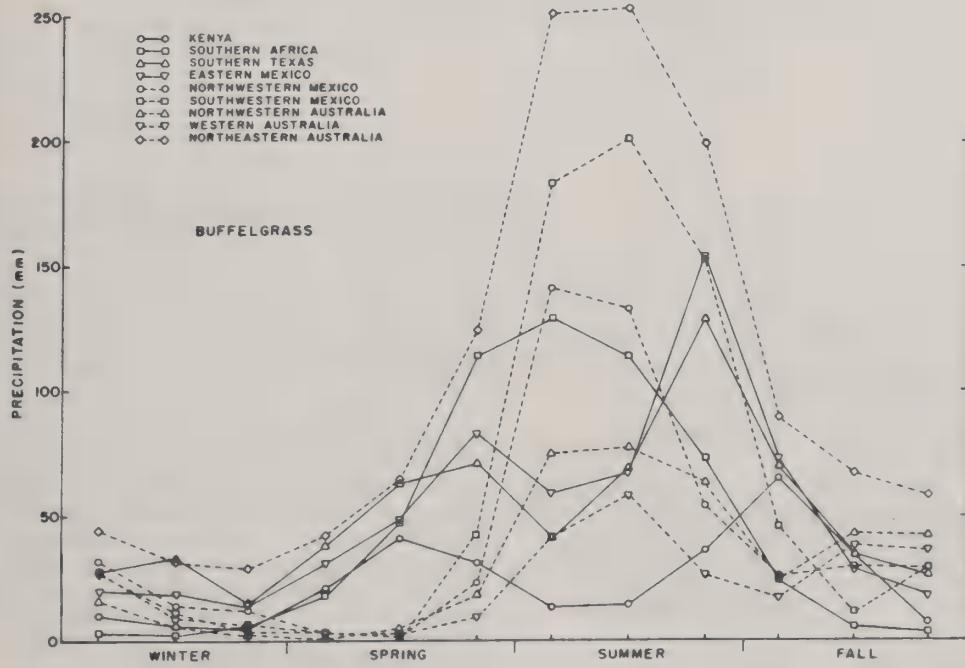

Figure 2. Mean monthly precipitation during winter, spring, summer, and fall where buffelgrass has been successfully established in the northern and southern hemispheres.
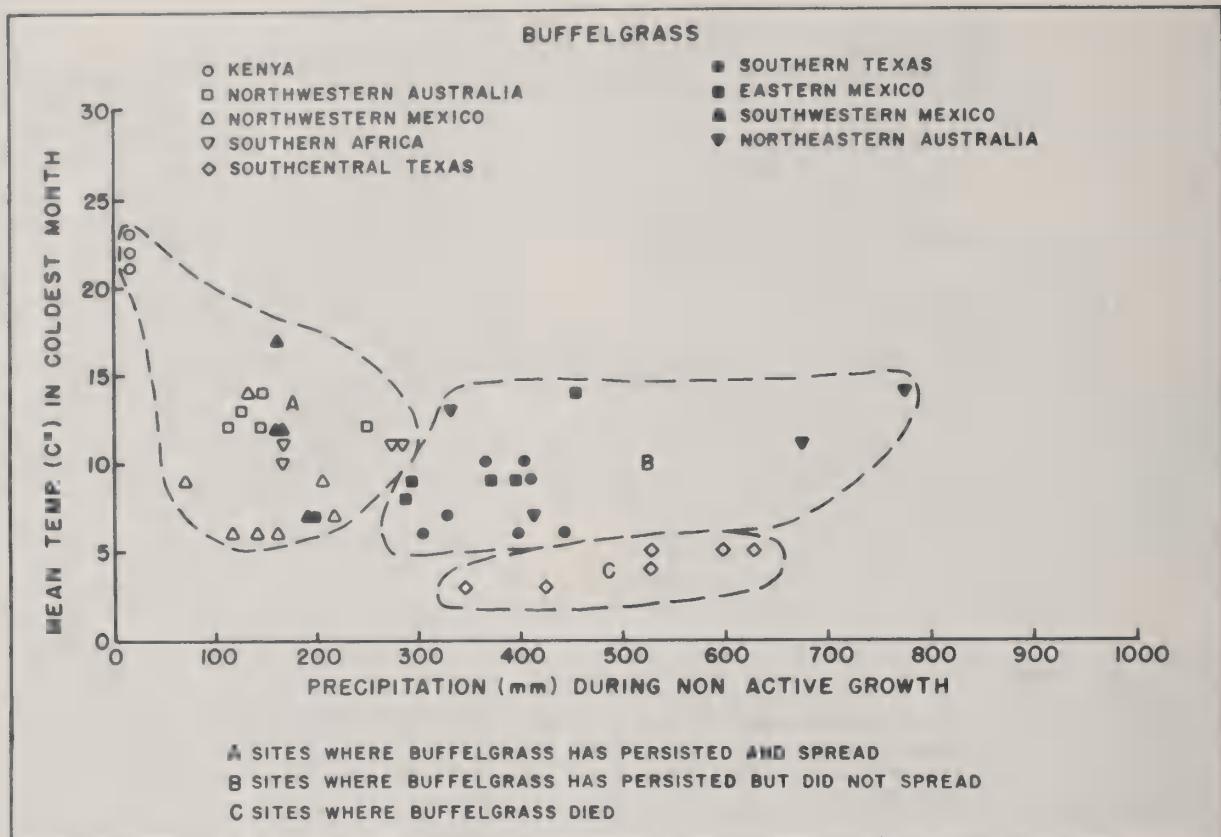
Figure 3. The effect of mean winter temperature and winter precipitation on the long-term persistence of buffelgrass in the northern and southern hemispheres.

Oklahoma and northwestern Texas, however, did persist and between 1940 and 1980 A-67 weeping lovegrass was established on 800,000 ha.

In 1947 and 1953 seed from collections in Oklahoma were transported to Argentina and plants were established on 800,000 ha (Covas and Carinie 1985). Seed were also transported and established in southeastern Australia (Lloyd et al. 1983, Watt 1983), southern Africa (Kruger and Grunow 1983, Kategile 1985), Japan (Nada 1985) and Spain (Nieto 1985).

Three major weeping lovegrass types, selected for leafiness and cold tolerance, have been and are currently being compared to A-67. 'Morpa' (more palatable) was collected by R.K. Godfrey, Bureau of Plant Industry, U.S. Department of Agriculture, at Rietvlei Plant Introduction Station near Pretoria in 1953. Seed were planted at Woodward, Oklahoma in 1954, and seed from mature plants that survived a harsh winter in 1955 - 1956 were increased (Voigt 1971). Morpa is taller, leaves are wider, and plants mature earlier than A-67 (Novosad et al. 1973). Beef cattle and sheep prefer Morpa and gain weight faster than when grazing A-67 (Shoop et al. 1976).

'Ermelo', a leafy weeping lovegrass type was collected 200 km southeast of Pretoria at Nooitgedacht Research Station in 1944. Elevation is 1,750 m and nighttime temperatures are frequently below freezing in fall, winter, and spring. Ermelo was introduced into the United States in 1948, and a second ecotype from an Ermelo seeding in Zimbabwe was introduced in 1964.

Weeping lovegrass seeds collected from 54 sites in Basutoland (currently Lesotho) were increased by the Department of Agriculture and Technical Services in Pretoria, and shipped to the United States in 1964. One selection was more palatable and vigorous than the others. 'Renner' has blue-green leaves and leaves are broader than A-67, Ermelo and Morpa. Renner was released in 1972 by the Texas Research Foundation (Read et al. 1980).

Differences among the four weeping lovegrass types, which do not include all African types, are related to leaf size, vigor, palatability and possible cold tolerance. The four types, however, represent most of the potential variability within the weeping lovegrass complex (Kruger and Grunow 1983). Thus, all types will be considered as one in our discussion.

In northcentral Tanzania where weeping lovegrass occurs, elevations vary from 1,190 to 1,530 m. Mean monthly minimum and maximum temperatures range from 10 to 18°C and 25 to 30°C, respectively (Fig. 4). Rainfall is bimodally distributed in summer and fall, and annually varies from 625 to 1,075 mm. More than 80% of the annual rainfall (765 to 965 mm) occurs when mean minimum daily temperatures are 15°C, and winter and spring are typically cool and dry. Weeping lovegrass generally grows in deep sand or loamy sand. Leaf growth occurs when early summer rains begin, productivity peaks in mid-summer just prior to or during a moderate dry period, and regrowth occurs in fall (Mukurasi 1984).

Weeping lovegrass has been successfully established from seed in southern Africa, southcentral Argentina and southcentral United States, but the species does not actively colonize adjacent nonplanted sites. In South Africa, on the Natal Highlands and Northern Transvaal Plains, weeping lovegrass has been established at 700 to 1,750 m elevations; while in Argentina plants are most often established at 80 to 310 m elevations. Winters in Tanzania, South Africa and Argentina are cold and dry (Fig. 4), but mean minimum winter temperatures in Tanzania are 8 to 10°C warmer than in South Africa and Argentina.

Rainfall in South Africa peaks in mid-summer and annually varies from 500 to 1,200 mm; while rainfall in Argentina peaks in early and late summer, and annually varies from 640 to 955 mm (Fig.5). Rainfall in the growing season ranges from 400 to 775 mm, at both locations, and mean maximum summer temperatures rarely exceed 30°C. Plant growth occurs when soil moisture is available and mean minimum temperatures rise above 10°C, and productivity peaks in mid-summer when mean minimum and maximum temperatures vary between 15 and 30°C (Kruger and Grunow 1983, Rethman and de Witt 1984, Covas and Cairnie 1985).

In the United States, weeping lovegrass has been established from southern Colorado to southern Arizona and from Maryland to Georgia (Crider 1945, Denman et al. 1953). Plant persistence, however, is limited to 300 to 1,000 m elevations in western Oklahoma, and northwestern and northcentral Texas. Plant growth begins in late spring when mean minimum temperatures rise above 10°C, productivity peaks when mean minimum and maximum temperatures range between 15 and 30°C, growth declines in mid-summer when mean maximum temperatures exceed 30°C and soils dry (Shoop and McIlvain 1970).

In western Oklahoma and northwestern and northcentral Texas, mean minimum daily temperatures in the coldest month vary from -1 to -5°C (Fig. 6) and minimum daily temperatures in winter are below 0°C for 60 to 90 days. Under such conditions established weeping · lovegrass stands will persist if they are not fertilized and defoliated prior to freezing winter temperatures (Rommann and McMurphy 1974). To the north in southern Kansas and west in southeastern Colorado mean minimum temperatures in the coldest month vary from -7 to -10°C and daily minimum temperatures are below 0°C for 120 to 160 days. Weeping lovegrass can be established during summer in Kansas and during atypically wet summers in Colorado, but plants die in winter (Dwyer et al. 1974, Dalrymple 1976, Shoop et al. 1976, Read et al. 1980, Novosad et al. 1983). Stands can also be
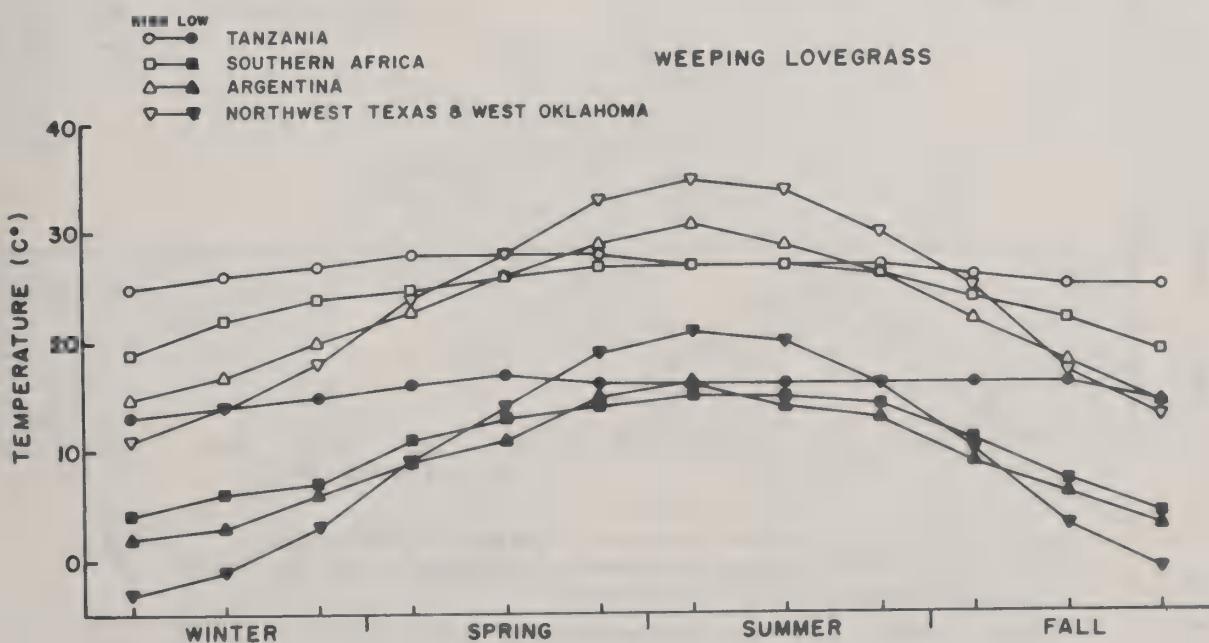

Figure 4. Mean monthly maximum and minimum temperatures during winter, spring, summer and fall where weeping lovegrass has been successfully established in the northern and southern hemispheres.
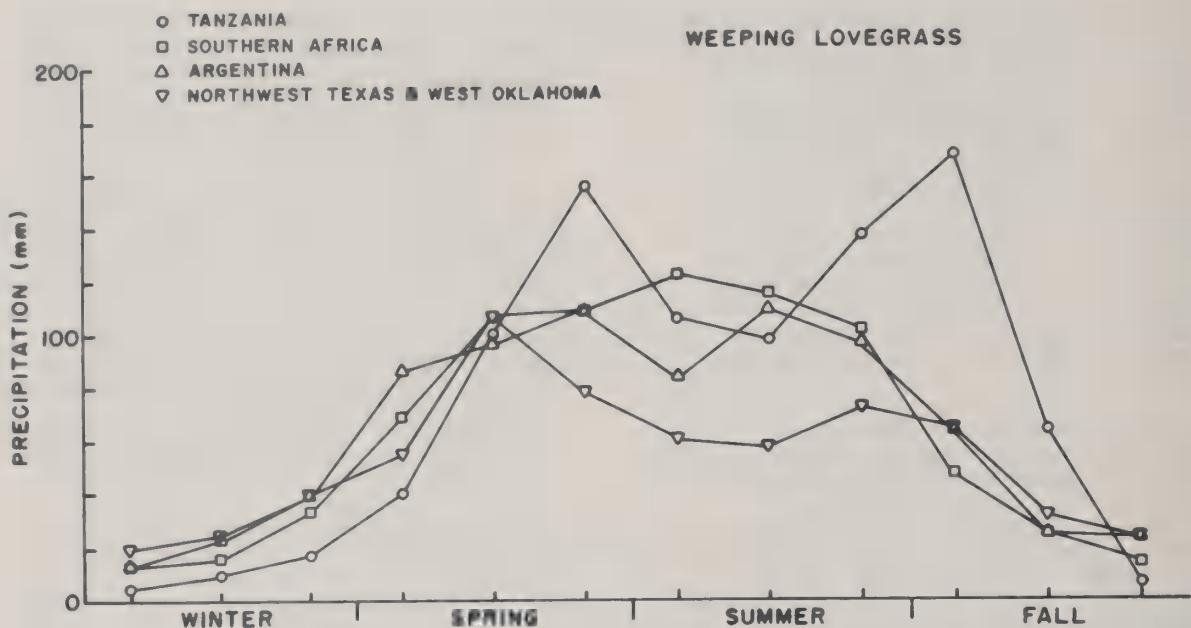
Figure 5. Mean monthly precipitation during winter, spring, summer, and fall where weeping lovegrass has been successfully established in the northern and southern hemispheres.
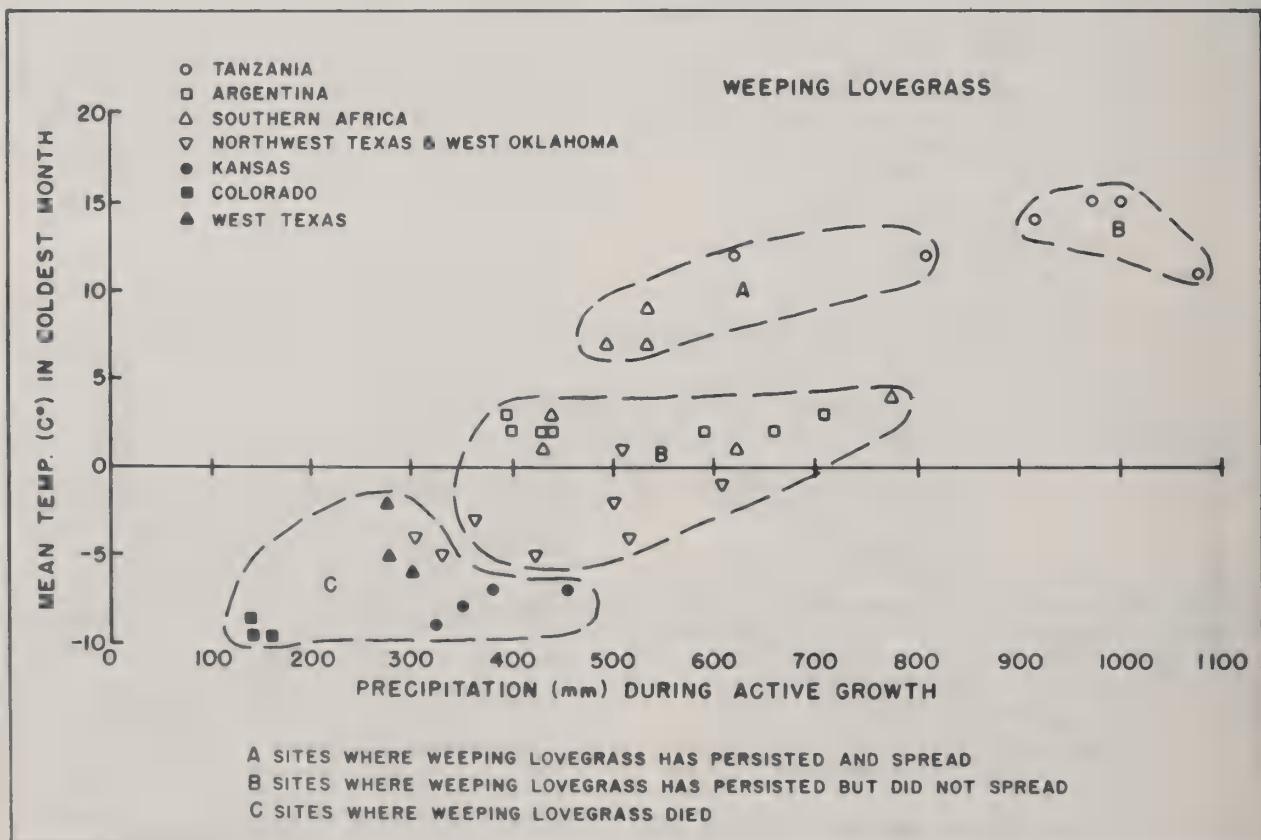

A SITES WHERE WEEPING LOVEGRASS HAS PERSISTED AND SPREAD
B SITES WHERE WEEPING LOVEGRASS HAS PERSISTED BUT DID NOT SPREAD
C SITES WHERE WEEPING LOVEGRASS DIED

Figure 6. The effect of mean winter temperature and summer precipitation on the long-term persistence of weeping lovegrass in the northern and southern hemispheres.

established during atypically wet summers and they persist for 10 or more years in southern Arizona, eastern New Mexico, and west Texas (Cox et al. 1982), but mature plants die when summer rainfall declines to 350 mm (Bridges 1941, Judd and Judd 1976).

Weeping lovegrass has been used throughout the world to revegetate mine spoils and steep slopes (Cresswell 1973, Farrington 1973, Wang et al. 1975, Voigt et al. 1982). Established stands persist where summer rainfall varies from 400 to 1,000 mm, and mean minimum and maximum temperatures annually vary from 0 to 30°C. Plant production, however, declines where summer rainfall exceeds 750 mm because of allelopathy (Dalrymple and Rogers 1983), competition with other forbs and grasses (Giraudo et al. 1984), fungal infections (van der Merwe et al. 1979), mites (Ehara 1985) and nematodes (Gnanapragasam 1981, van den Berg 1985).

Kleingrass

Dr. Mildred Wilman, Director of the McGregor Museum, Kimberley, Union of South Africa, collected kleingrass seed between Kimberley in the Orange Free State and Potchefstroom in the Transvaal in 1949. Seed from the collections were planted throughout Texas, United States, between 1954 and 1968. Plants from seed numbered 166400 were successfully established in central Texas, and in 1968 U.S. Department of Agriculture, Soil Conservation Service and Texas Agricultural Experiment Station jointly released 'Selection 75' (Holt 1969).

Between 1975 and 1985, commercial seed producers in Texas sold over 2 million kg of Selection 75 seed, and seed were planted on 2.8 million ha of degraded rangeland. Seed were transported and established on small acreages in eastern Australia (Rees 1972), Brazil (Alberto and Barreto 1983), Cuba (Oquendo et al. 1983), India (Mukherjee 1972), Japan (Inosaka et al. 1975), Venezuala (Gallardo and Leone 1983) and Zimbabwe (Mills 1977).

Kleingrass variety makarikariense, originally collected in Botswana, has a bluish color and wider leaves than Selection 75 (Holt et al. 1985). Makarikariense has been successfully established on small acreages in eastern Australia (Lloyd et al. 1983), Brazil (Alberto and Barreto 1983), and Japan (Inosaka et al. 1975). Selection 75 is apparently more cold tolerant than makarikariense, but their establishment, productivity and digestibility characteristics under moisture stress are similar (Kobayashi et al. 1978, Mackenzie et al. 1982, Bade et al. 1985). Thus, both selections are considered as one in our discussion.

Elevations in the western Transvaal of South Africa range from 1,000 to 1,450 m, and mean monthly minimum and maximum temperatures annually vary from -2 to 17°C and 16 to 31°C (Fig. 7), respectively. Rainfall peaks in summer, and annually varies from 425 mm at Kimberley to 610 mm at Potchefstroom. Winters are dry, and mean minimum daily temperatures in the coldest month vary from 0 to 4°C. In Zimbabwe, 200 to 300 km north, kleingrass grown under a similar climatic regime initiated growth
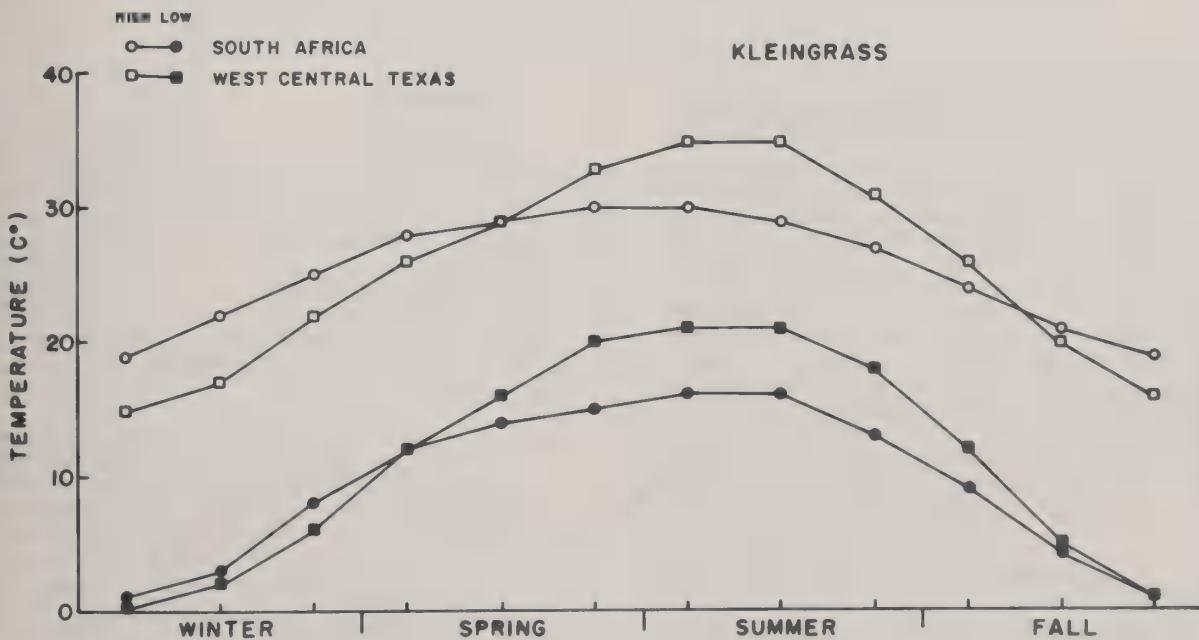

Figure 7. Mean monthly maximum and minimum temperatures during winter, spring, summer and fall where kleingrass has been successfully established in the northern and southern hemispheres.

in spring when temperatures approached 10°C and moisture in the soil was available (Rodel and Boultwood 1981). Plant productivity peaked when mean daily minimum and maximum temperatures ranged from 15 to 30°C, and seedlings and mature plants were most often found where fine soil particles and water accumulated (Rodel 1972).

Kleingrass has been successfully established from seed in Australia (Rees 1972), Brazil (Alberto and Barreto 1983), Japan (Kobayashi el al. 1978), United States (Holt 1969), Venezuela (Gallardo and Leone 1983) and Zimbabwe (Rodel 1972), but the species does not actively colonize adjacent non-planted sites. The species can be expected to survive extreme fall defoliation only in west central Texas, United States (Holt et al. 1985) and southern Africa (Rodel and Boultwood 1981).

In west central Texas, elevations range from 440 to 540 m, and mean minimum and maximum temperatures annually vary from 0 to 22°C and 12 to 36°C (Fig. 7), respectively. Winters are dry in some years while wet in others, and mean minimum daily temperatures in the coldest month vary from 0 to 2°C. Rainfall is bimodally distributed, and peaks occur in late spring and early fall (Fig.8). If soil moisture is available kleingrass grows from spring to fall when mean minimum daily temperatures are above 10°C. Plant productivity peaks throughout summer when mean maximum temperatures range from 30 to 36°C (Stubbendieck et al. 1973, Pitman and Holt 1983, Bade et al. 1985, Bedunah and Sosebee 1985). Weeping lovegrass productivity, under similar temperature extremes, rapidly declines even when soil moisture is available (Farrington 1973, Mills 1977, Covas and Cairnie 1985).

Kleingrass persistence is limited by temperature to the north and by precipitation west of west-central Texas (Taliaferro et al. 1983), while production is limited by competition to the east and south (Holt et al. 1985). Established kleingrass stands in northern Texas and Oklahoma die (Holt 1969) where mean minimum daily temperatures in the coldest month vary from -1 to -5°C (Fig. 9) and minimum daily temperatures in winter are below 0°C for 30 to 60 days; whereas in west Texas, stands die if total precipitation in the growing season (April to October) is less than 400 mm (Pratt et al. 1971). Kleingrass can be successfully established and will persist in high rainfall (700 to 990 mm) areas of east and south Texas, but competition with other seeded grasses reduces kleingrass forage production (Hussey and Holt 1982). Production in high rainfall areas may also be limited by nematodes (Rodel et al. 1976).

Toxins accumulate in kleingrass foliage, and goats and sheep may die after consuming large quantities during fall in southern Africa (Rodel 1972) and summer and fall in central Texas (Dollahite et al. 1977, Muchiri et al. 1980). The distribution of kleingrass, as a potential pasture grass, may be limited because of its toxic characteristics.
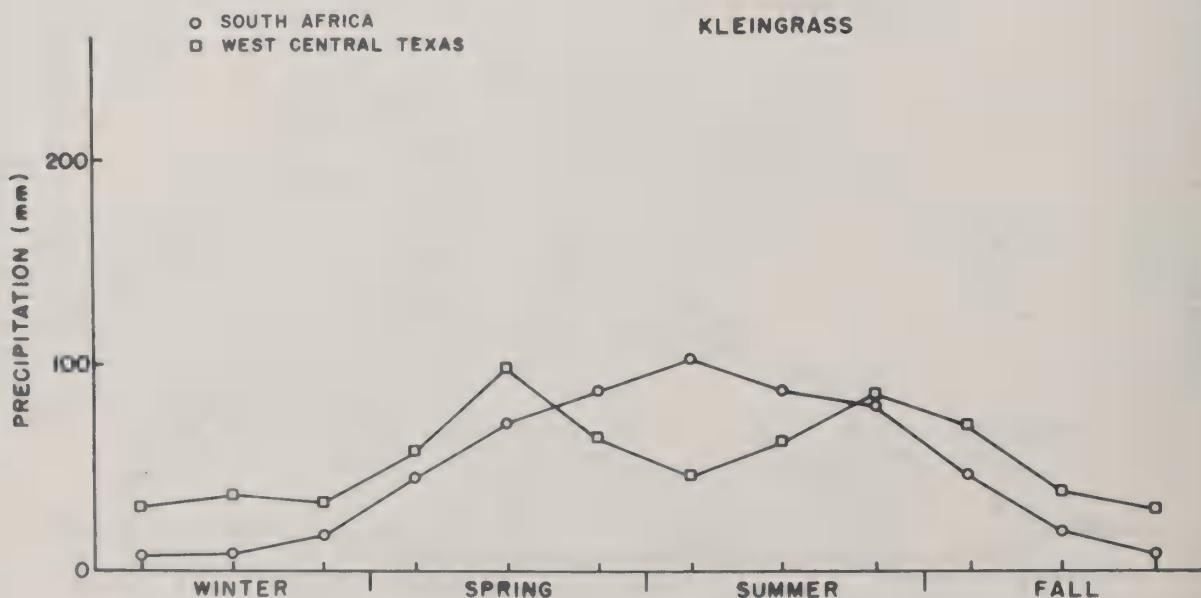

Figure 8. Mean monthly precipitation during winter, spring, summer, and fall where kleingrass has been successfully established in the northern and southern hemispheres.

KLEINGRASS

○ SOUTHERN AFRICA
□ WESTCENTRAL TEXAS
△ NORTHERN TEXAS
▽ SOUTHERN TEXAS

MEAN TEMP. C° IN COLDEST MONTH

PRECIPITATION (mm) DURING ACTIVE GROWTH

A NO SITES WERE FOUND WHERE KLEINGRASS HAS PERSISTED AND SPREAD
B SITES WHERE KLEINGRASS HAS PERSISTED BUT DID NOT SPREAD
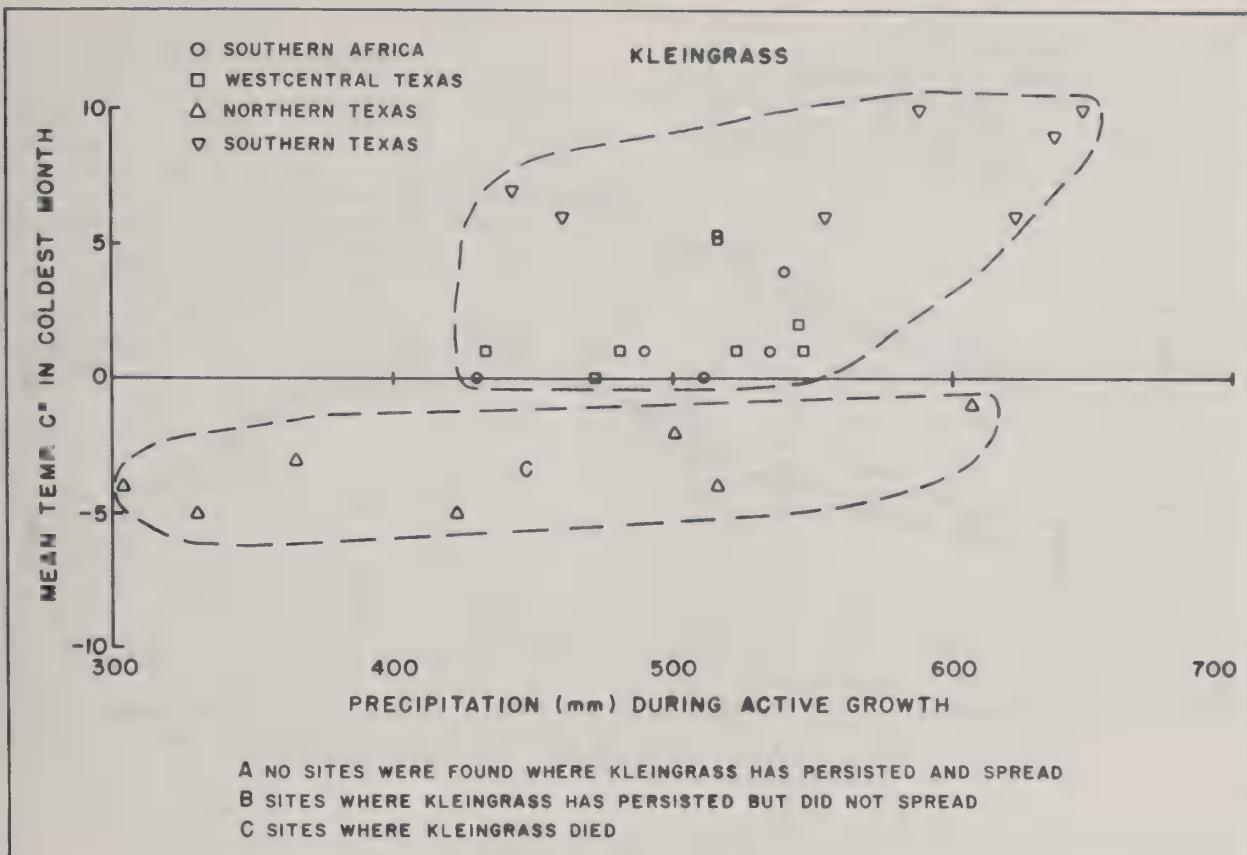C SITES WHERE KLEINGRASS DIED

Figure 9.   The effect of mean winter temperature and summer precipitation
on the long-term persistence of kleingrass in the northern and
southern hemispheres.

Lehmann Lovegrass

Dr. Mildred Wilman, Director of the McGregor
Museum, Kimberley, Union of South Africa, sent
Lehmann lovegrass seed collected in the
Griqualand West Region of South Africa to F.J.
Crider at Superior, Arizona, United States in
1932 (Crider 1945). In 1935, Crider organized a
series of irrigated screening tests at Tucson,
Arizona and selected plants that matured quickly
and produced seed in the first growing season.
Seeds from established plants were numbered 'A-
68'.

Between 1937 and 1950, approximately 135 kg of
Lehmann lovegrass seed, produced at Tucson, was
planted in small plots from west Texas to
Arizona (Cox et al. 1982). Many of the seedings
were successful, and between 1951 and 1985,
commercial seed growers produced more than
75,000 kg of Lehmann lovegrass seed (Cox and
Ruyle 1986). Approximately 70% of the seed was
sown on rangelands in Arizona, New Mexico, and
Texas. The majority of the remaining seed was
transported into Mexico and planted in the
northern frontier states of Chihuahua, Coahuila
and Sonora (Cota and Johnson 1975, Sanchez 1976,
Cox et al. 1982). Between 1940 and 1980,
ranchers and government agencies successfully
established Lehmann lovegrass on more than
70,000 ha in the southwestern United States and
northern Mexico (Cox and Ruyle 1986).

Elevations in west-central South Africa where
Lehmann lovegrass occurs naturally, range from
1,175 to 1,350 m and mean minimum and maximum
temperatures annually vary from 0 to 19°C and 18
to 34°C (Fig. 10), respectively. Annual
rainfall peaks in late summer, and approximately
80% (225 to 395 mm) is distributed in late
spring, summer and early fall when mean minimum
daily temperatures are above 15°C. Rainfall
amounts are low and storms are widely
distributed in late spring and summer, and
Lehmann lovegrass normally remains semidormant.
As rainfall amount and distribution increase in
late summer, Lehmann lovegrass initiates growth
and productivity peaks in 30 to 40 days (Fourie
and Roberts 1976). Precipitation during active
growth ranges from 130 to 160 mm (Fig. 11) while
mean minimum and maximum temperatures vary from
15 to 32°C.

Where Lehmann lovegrass has been successfully
established in the southwestern United States
and northern Mexico, elevations range between
775 and 1,540 m, and daily mean minimum and
maximum temperatures vary annually from -4 to
20°C and 13 to 38°C, respectively (Fig. 10).
Annual rainfall varies from 275 to 500 mm, and
may be distributed in a summer peak or bimodally
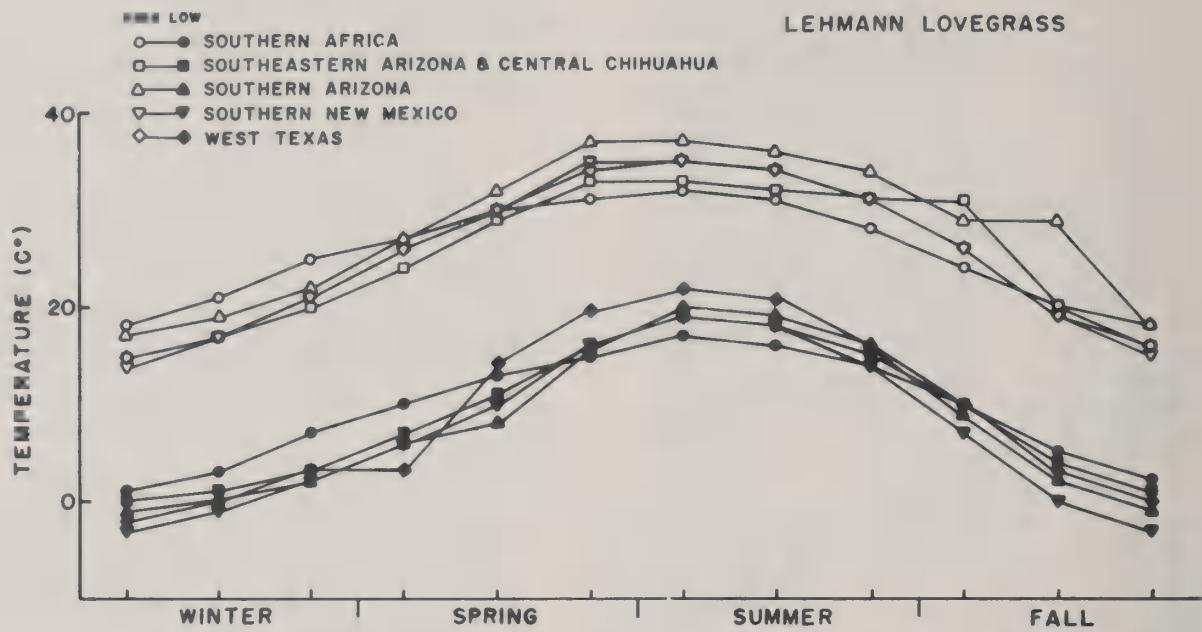in summer and winter (Fig. 11).

Figure 10. Mean monthly maximum and minimum temperatures during winter, spring, summer and fall where Lehmann lovegrass has been successfully established in the northern and southern hemispheres.
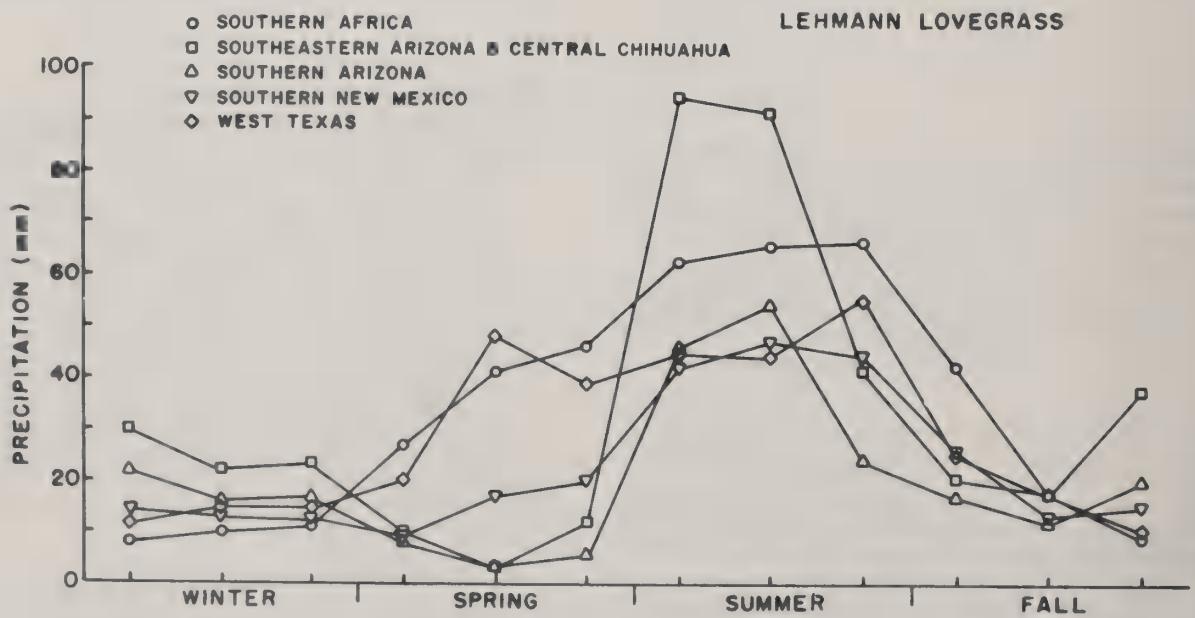
Figure 11. Mean monthly precipitation during winter, spring, summer and fall where weeping lovegrass has been successfully established in the northern and southern hemispheres.

Lehmann lovegrass seed, from plants established on planted sites, actively colonize adjacent nonplanted sites in southeastern Arizona (Cox and Ruyle 1986) and northcentral Mexico. At all locations, summer rainfall during active plant growth ranges from 150 to 220 mm (Fig. 12), and elevations vary from 1,100 to 1,540 m (Anderson et al. 1957, Cable 1971). Where Lehmann lovegrass has persisted but has not spread in southeastern Arizona, southern New Mexico, west Texas, and northern Mexico, summer rainfall during active growth is about 100 mm. Established Lehmann lovegrass stands in the area die when summer rainfall during active growth ranges between 70 and 85 mm.

Effects of Soil Texture

Buffelgrass, kleingrass, weeping and Lehmann lovegrasses have been initially established in almost all soil textural types; but long-term persistence of each grass is dependent on specific textural types (Fig. 13). Buffelgrass and kleingrass seedlings emerge when seed are sown in sandy, silty, and clayey soils, but buffelgrass emergence declines as either sand, silt, or clay content approaches 100% (Mutz and Scifres 1975, Agostini et al. 1981). Buffelgrass seedlings gradually lose vigor and die when established in silt, silt loam, silty clay loam, silt clay and clay soils; whereas, kleingrass seedling persist in the same soils (Humphreys 1967, Cota and Johnson 1975, Sweeney and Hopkins 1975, Watt 1976, Christie 1978, Pitman et al. 1981, Rodel et al. 1981, Hanselka 1985). Buffelgrass persists in well drained loam, sandy loam, clay loam and sandy clay loam soils, and actively spreads by seed in northwestern Australia and northwestern Mexico in sandy loam soils (Humphreys 1967, Cota and Johnson 1975).

Weeping lovegrass seedlings emerge from sand, loamy sand, sandy loam, and loam soils, but long-term persistence in southern Africa is normally limited to deep sandy soils (Rethman and de Witt 1984). Sand depth may vary from 1 to 5 m (Farrington 1973, Wang et al. 1975, Kruger and Grunow 1983), and the soil profile may be saturated seasonally (Covas and Cairnie 1985).

In the eastern and southern United States weeping lovegrass can be established and will persist in sandy soil (Dalrymple 1976, Haferkamp and Mutz 1982). Plant distribution in this area, however, is limited by soil texture which is predominantly silt loam, clay and clay loam.
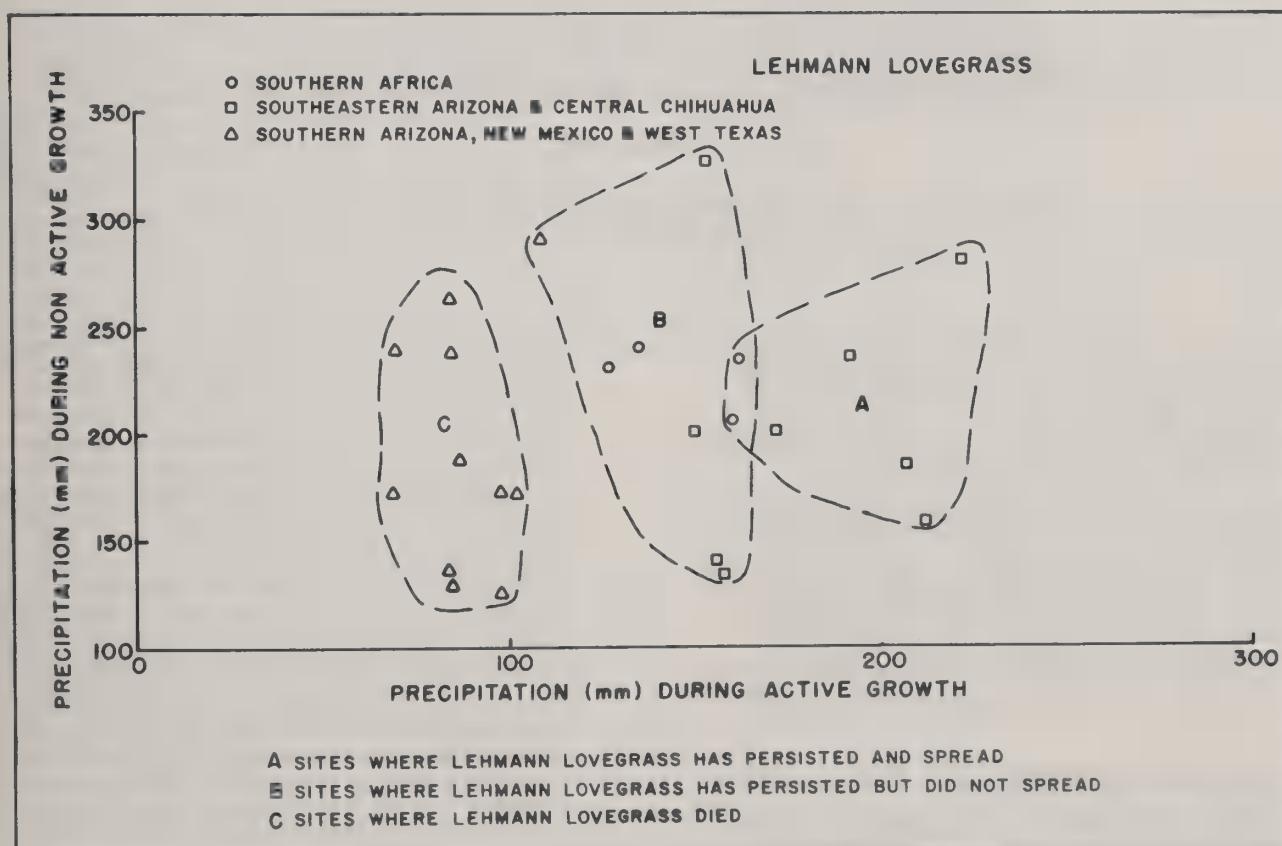

Figure 12. The effect of winter and summer precipitation on the long-term persistence of Lehmann lovegrass in the northern and southern hemispheres.
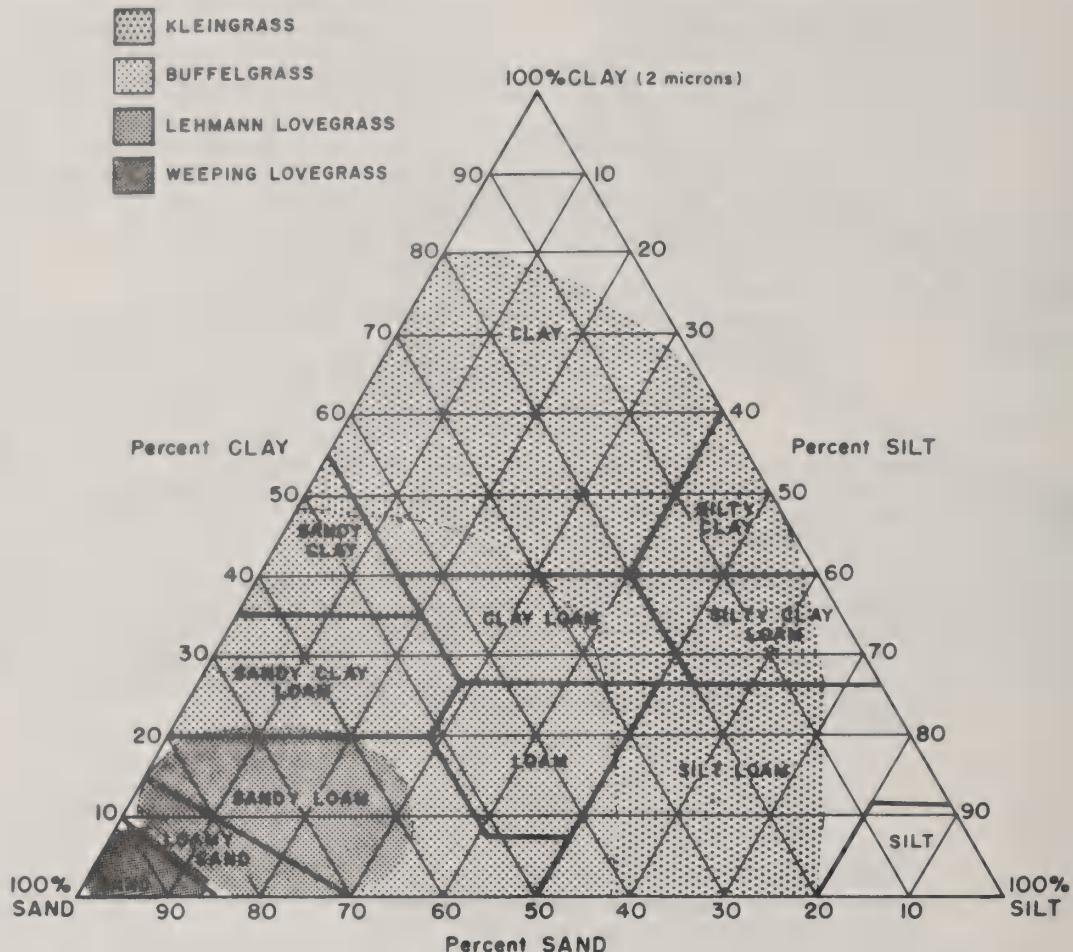
Figure 13. The effect of soil texture on the long-term persistence of
four warm-season African grasses.

Chemical and physical characteristics of these
soil types either reduce or inhibit weeping
lovegrass germination (Stubbendieck 1974),
seedling emergence (Cox et al. 1986), shoot
growth (Chichester 1981, Lavin et al. 1981) and
root growth (Tischler and Voigt 1983).

Lehmann lovegrass seedlings emerge when seeds
are planted near the surface in sand, loamy
sand, and sandy loam soils; seedlings, however,
do not emerge in silt loam, loam and clay loam
soils, regardless of planting depth (Cox et al.
1983b, Cox et al. 1984). In southeastern
Arizona and northcentral Mexico long-term
persistence and spread is limited to loamy sand
and sandy loam soils (Cox and Ruyle 1986).

SUMMARY AND CONCLUSIONS

Attempts to artificially revegetate degraded
rangelands in the northern and southern
hemispheres have been going on for approximately
100 years (Humphreys 1967, Cox et al. 1982).
The approach most often used was to: (1)
mechanically reduce unwanted competition, (2)
prepare a seedbed, (3) plant seeds of as many

species, accessions and cultivars in as many
soils as possible, and (4) pray for rain. The
technique has been successful, but an
established stand could only be expected in 1 of
every 10 plantings. The situation became
confused, however, when positive results,
obtained at atypical sites or in atypical years,
were extrapolated. In addition, it was not
possible to compare results because: (1) on-
site weather data were not collected, (2) new
seedbed methods were not compared with a
standard, (3) trials were unreplicated in time
and space, (4) data collection techniques
differed among individuals, and (5) common seed
sources were often incorrectly identified. The
situation can be compared to betting at the
local race track: you lose most of the time,
hope for a long-shot to win, and never
understand the factors which contributed to the
outcome.

Cox et al. (1982) discussed the problems
associated with artificial seeding in the
southwestern United States and northern Mexico.
Between 1890 and 1980, more than 300 species
were planted at 400 locations, and the presented
results show or infer that 83 species were

successfully established. Planting site evaluation and discussion with some authors, however, indicated that only 14 species were adapted. Field evaluations to determine ease of establishment, persistence and potential spread under existing climatic and edaphic conditions clearly indicated that only two species (buffelgrass and Lehmann lovegrass) were adapted.

In the Sonoran Desert of the southwestern United States and northwestern Mexico, buffelgrass and Lehmann lovegrass have been widely seeded, and both have spread to adjacent nonplanted sites. Since buffelgrass and Lehmann lovegrass produce green leaves during the mild and wet winters, Cox et al. (1986) and Cox and Ruyle (1986) concluded that winter growth was necessary for plant survival. Their conclusions were based on climatic summaries from only North American stations, and appeared to be correct. Climatic summaries for the northern and southern hemispheres, presented in this paper, show that their conclusions were incorrect because winter rain does not occur in Africa where the two grasses are currently found.

Our attempt to identify relationships between mean monthly temperatures and rainfall, soil texture, and the persistence and spread of four African grasses is a first approximation and needs refinement. Graphical presentations, however, show potential relationships that may influence persistence. For example, the distribution of buffelgrass, kleingrass and weeping lovegrass is limited when mean minimum temperatures in the coldest month are 5°C or less, 0°C or less and -5°C or less, respectively. On sandy or sandy loam surface soils, Lehmann lovegrass stands: (1) die if summer rainfall in 30 to 45 days is less than 90 mm, (2) persist but do not spread between 91 and 125 mm, and (3) spread between 126 and 220 mm. Whereas, buffelgrass requires approximately 90 days of summer growth and relatively warm dry winters to colonize sandy loam soils. In contrast, kleingrass and weeping lovegrass require a 150 to 180 day summer growing season to spread on silty, clayey, and sandy soils, respectively.

We realize that long-term temperature and rainfall means do not reflect the extremes which are critical for seed germination, seedling growth and mature plant survival. This study deals with representative climate over areas rather than points, and since temperature and rainfall extremes seldom occur over large areas (Palmer 1964), the means probably do not depart from conditions which limit or perpetuate a species. We also recognize that topography at the climatic station differs from the actual site where established stands either died, persisted or spread. This does not appear to represent a serious departure from reality where the landscape is relatively flat, but where topography changes dramatically over a relatively short distance values at the climatic station may not adequately represent planting sites at higher or lower elevations. Irrespective of these inherent problems, the presented approach will be usefull in reducing the risks currently associated with artificial revegetation on degraded rangelands of the world.

LITERATURE CITED

Alberto, G. and I.L. Barreto 1983. Comparison between cultivators of Panicum maximum and Panicum coloratum under the effects of legumes and rates of nitrogen. Revista da Sociedade Brajileira de Zootecnia 12:440-457. [In Portuguese]

Anderson, D., L.P. Hamilton, H.G. Reynolds, and R.R. Humphrey 1957. Reseeding desert grasslands in southern Arizona. Arizona Agr. Exp. Sta. Bull. 249.

Agostini, J.J., J.A. Morales, and D. Emkerlins 1981. Yield and quality of two hybrids of buffelgrass (Cenchrus ciliaris) damaged by different populations of the spittlebug (Aneolamia albofasciata) and mites (Prosapia simulans). Agronomia 200:42-47. [In Spanish]

Azmi, M.I. and A. Singh 1985. Pathogenicity of Tylenchorhynchus vulgaris on Anjan grass, Cenchrus ciliaris cv. Igfri-S-3108. Indian J. Nematology 14:184-185.

Bade, D.H., B.E. Conrad and E.C. Holt 1985. Temperature and water stress effects on growth of tropical grasses. J. Range Manage. 38:321-324.

Bedunah, D.J. and R.E. Sosebee 1985. Influence of site manipulation on infiltration rates of depleted west Texas range sites. J. Range Manage. 38:200-205.

Bogdan, A.V. 1961. Breeding behavior of Cenchrus ciliaris in Kenya. East Afr. Agr. and For. J. 26:241.

Bridges, J.O. 1941. Reseeding trials on arid range. New Mexico Agr. Exp. Sta. Bull. No. 278.

Brooks, G.B. 1929. Queensland Department of Agriculture and Stock Annual Report, 1928-1929. Brisbane.

Cable, D.R. 1971. Lehmann lovegrass in the Santa Rita Experimental Range, 1937-1968. J. Range Manage. 24:17-21.

Chichester, F.W. 1981. Preliminary evaluation of forage grass growth on mine spoil materials from an east central Texas site. 1. Overburden strata. Soil Sci. 132:204-212.

Christie, E.K. 1978. Ecosystem processes in semiarid grasslands. I. Primary production and water use of two communities processing different photosynthetic pathways. Aust. J. Agr. Res. 29:773-787.

Cooke, R.U. and R.W. Reeves 1976. Arroyos and environmental change in the American Southwest. Oxford Press, London.

Cota, A. and D. Johnson 1975. Adaptation and production of ten perennial grass species in Sonora. Pastizales-CI-MP-001. [In Spanish]

Covas, G. and A.G. Cairnie 1985. Weeping lovegrass; A basic information manuel for its establishment and utilization under normal conditions. Editorial Hemisferio Sur S.A., Buenos Airea. [In Spanish]

Cox, J.R., H.L. Morton, J.R. Johnson, T.N. Jordan, G.L. Martin, S.C., and L.C. Fierro 1982. Vegetation restoration in the Chihuahuan and Sonoran Deserts of North America. USDA, Agr. Res. Serv., Agr. Reviews and Manuals. ARM-W-28.

Cox, J.R., H.L. Morton, J.T. Labaume, and K.G. Renard 1983a. Reviving Arizona's rangelands. J. Soil and Water Cons. (USA) 38:342-345.

Cox, J.R., H.A. Schreiber, and H.L. Morton 1983b. The initial growth of two range grasses collected on nonfertilized and fertilized soils collected from creosotebush communities in the southwestern United States. J. Range Manage. 36:726-729.

Cox, J.R., J.M. Parker, and J.L. Stroehlein 1984. Soil properties in creosotebush communities and their relative effects on the growth of seeded range grasses. Soil Sci. Soc. Amer. J. 48:1442-1445.

Cox, J.R., M.H. Martin-R., F.A. Ibarra-F., and H.L. Morton 1986. Establishment of range grasses on various seedbeds at creosotebush (Larrea tridentata) sites in Arizona U.S.A., and Chihuahua, Mexico. J. Range Manage. 39:540-546.

Cox, J.R., and G.B. Ruyle 1986. Influence of climatic and edaphic factors on the distribution of Eragrostis lehmanniana Nees in Arizona, U.S.A. J. Grassl. Soc. sth. Afr. 3:25-29.

Cresswell, C.F. 1973. Changes in vegetational composition, nutritional status, soils, and microbial populations with the establishment of vegetation on gold-mined dumps on the Witwatersrand. p. 335-359. In R.J. Hutnik and G. Davis (ed.). Ecology and reclamation of devastated land. Gordon and Breach Co., New York.

Crider, F.J. 1945. Three introduced lovegrasses for soil conservation. U.S. Dep. Agr. Circular 730.

Dalrymple, R.L. 1976. Bermudagrass and weeping lovegrass mixtures for forage. The Samuel Roberts Noble Foundation, Agr. Div. No. BWL-76. Admore, OK.

Dalrymple, R.L., and J.L. Rogers 1983. Allelopathic effects of western ragweed on seed germination and seedling growth of selected plants. J. Chem. Ecology 9:1073-1078.

Das, R.B., G.N. Bhati, and V.D. Joshi 1978. Plant growth rhythm and protein status of desert forage grasses: Cenchrus ciliaris and Panicum antidotale. Forage Research 4:97-99.

Denman, C.E., W.C. Elder, and V.G. Heller 1953. Performance of weeping lovegrass under different management practices. Oklahoma Agr. Exp. Sta. Tech. Bull. No. T-48.

Dollahite, J.W., R.L. Younger, and L.P. Jones 1977. Photosensitization in lambs grazing kleingrass (Panicum coloratum). J. Amer. Vet. Med. Ass. 171:1264-1265.

du Toit, J., J.W. Rabie, and J.O. Grunow 1973. Nutritional production studies on Cenchrus ciliaris L. c.v. Molopo. Proc. Grassl. Soc. sth. Afr. 8:107-115. [In Afrikaans]

Dye, P.J. and B.H. Walker 1980. Vegetation - environment relations on sodic soils of Zimbabwe Rhodesia. J. Ecology 68:589-606.

Dwyer, D.D., P.L. Sims, and L.S. Pope 1974. Preference of steers for certain native and introduced forage plants. J. Range Manage. 17:83-85.

Ehara, S. 1985. Five species of phytoseiid mites from Japan with descriptions of two new species (Acarina, Phytoseiidae). Zoological Sci. 2:115-121.

Farrington, P. 1973. The seasonal growth of lovegrass (Eragrostis curvula) on deep sandy soils in a semiarid environment. Aust. J. Exp. Agr. and Animal Husb. 13:383-388.

Fourie, J.H., and B.R. Roberts 1976. A comparative study of three veld types of the Northern Cape: Species evaluation and yield. Proc. Grassl. Soc. sth. Afr. 11:79-85.

Gallardo, A. and A. Leone 1983. Pasture evaluation in the desert zone of Venezuela for the development of goat production. p. 367-369. In J.A. Smith and V.W. Smith (ed.). Proc. XIV International Grassland Congress, held at Lexington, Kentucky, U.S.A. Westview Press, Boulder, CO.

Giraudo, C.G., C.A. Frasinelli, E. Verges, and A. Marchi 1984. Effect of paraquat on quality of deferred weeping lovegrass. Revista Argentina de Produccion Animal 4:43-49. [In Spanish]

Gnanapragasam, N.C. 1981. The influence of cultivation on Eragrostis curvula in nematode-infested soils, on the subsequent build-up of populations in replanted tea. Tea Quarterly 50:160-162.

Griffith, D. 1901. Range improvement in Arizona. USDA, Bureau of Plant Industry, Bull. No. 67.

Haferkamp, M.R., and J.L. Mutz 1982. Evaluation of grasses for selected sites in the south Texas plains. Texas Agr. Exp. Sta. MP-1507.

Hanselka, C.W. 1985. Grazing management strategies for buffelgrass. p. 53-64. In E.C.A. Runge and J.L. Schuster (ed.). Buffelgrass: Adaptation, management and forage quality Symposium. Texas Agr. Exp. Sta. MP-1575.

Harsh, L.N., C.M. Verma, and B.L. Jain 1981. Relationship between precipitation and forage production of Cenchrus ciliaris in arid regions. Annals Arid Zone 20:101-106.

Holt, E.C. 1969. Kleingrass 75. Texas Agr. Exp. Sta. TAP-518.

Holt, E.C. 1985. Buffelgrass - A brief history. p. 1-5. In E.C.A. Runge and J.L. Schuster (ed.). Buffelgrass: Adaptation, management and forage symposium. Texas Agr. Exp. Sta. MP-1575.

Holt, E.C., M.A. Hussey, J.C. Read, and R.M. Jones 1985. Kleingrass cultivar evaluations. Texas Agr. Exp. Sta. PR-4263.

Humphreys, L.R. 1967. Buffelgrass (Cenchrus ciliaris) in Australia. Trop. Grassl. 1:123-134.

Hussey, M.A. and E.C. Holt 1982. Selection and evaluation of heavy seed\weight synthetic cultivars of kleingrass. Texas Agr. Exp. Sta. Cpr-4024.

Hussian, F., and I. Ilahi 1982. Some preliminary studies on the interference exhibited by Bothriochloa pertusa (L.) A Camus. Pakistan J. Botany 14:16.

Inosaka, M., K. Ito, H. Numaguchi, M. Aratani, and K. Maeda 1975. Studies on the productivity of some tropical grasses. I. Relationship between heading rate and dry matter yield under different cutting treatments. Japanese J. Trop. Agr. 18:87-92. [In Japanese]

Ivory, D.A., T.H. Stobbs, M.N. McLeod and P.E. Whiteman 1974. Effect of day and night temperatures on estimates dry matter digestibility of Cenchrus ciliaris and Pennisetum clandestinum. J. Aust. Institute Agr. 40:156-158.

Ivory, D.A., and P.C. Whiteman 1978. Effect of temperature on growth of five subtropical grasses. I. Effect of day and night temperature on growth and morphological development. Aust. J. Plant Physiology 5:149-157.

Judd, I.B. and L.W. Judd 1976. Plant survival in the arid southwest 30 years after seeding. J. Range Manage. 29:248-251.

Kategile, J.A. 1985. Pasture improvement research in eastern and southern Africa. International Development Research Center, Ottawa.

Khan, S.M. and R.M. Zarif 1982. Enhancing rage productivity through grass seeding in subtropical semiarid rangelands near Peshawar. Pakistan J. Forestry 32:89-94.

Kobayashi, T., S. Nishimura, and S. Tanaka 1978. Growth of tropical and subtropical grasses in the southwestern area of Japan as influenced by air temperature. I. Effects of sowing date, growth stage and cutting frequency on growth and yield. Sci. Bull. Faculty of Agr., Kyushu Univ. 32:169-175 (Fukuoka). [In Japanese]

Kruger, A.J. and J.O. Grunow 1983. Dry matter production and quality characteristics of 40 Eragrostis curvula ecotypes. Agroplantae 15:45-52. [In Afrikaans]

Lavin, F., T.N. Johnsen, JR. and F.B. Gomm 1981. Mulching, furrowing and fallowing of forage plantings on Arizona pinyon-juniper ranges. J. Range Manage. 34:171-177.

Lloyd, D.L., J.G. Nation, T.B. Hilder, and P.K. O'Rourke 1983. Productivity of grazed Makarikari grass - lucerne, Rhodesgrass - lucerne and lucerne pastures in the northern wheat belt of Australia. Aust. J. Exp. Agr. and Animal Husb. 23:383-392.

MacKenzie, J., R. Mayer, and W.J. Bisset 1982. Productivity of five subtropic grasses on a black earth of the eastern Darling Downs of Queensland. Trop. Grassl. 16:170-180.

Mills, P.F.L. 1977. Comparisons of the yield and palatability of Digitaria, Cynodon, Eragrostis, Panicum and Brachiaria species and cultivars when defoliated at different frequencies and heights at two sites. Rhodesia (Zimbabwe) Agr. J. 74:159-163.

Molina, S.I., T.R. Garza, and H.M. Torres 1976. Beef production on guinea and buffelgrasses with two fertilizer rates, during one year in Tizimin, Yucatan. Tecnica Pecuaria en Mexico 31:17-21. [In Spanish]

Muchiri, D.J., C.H. Bridges, D.N. Ueckert, and E.M. Bailey 1980. Photosensitization of sheep on kleingrass (Panicum coloratum) pasture. J. Amer. Vet. Med. Ass. 177:353-354.

Mukurasi, N.J. 1984. The response of tropical grasses to higher rates of nitrogen at Uyole, Tanzania. Lantbruksuniversitet 131:53-66.

Mukherjee, A. 1972. Effect of nitrogen on the growth of Panicum in sandy soil. Indian Agriculturist 16:199-200.

Mutz, J.L. and C.J. Scifres 1975. Soil texture and planting depth influence buffelgrass emergence. J. Range Manage. 28:222-224.

Nada, Y. 1985. Palatability and adaptability of ten tropical grasses used as grazing pasture in Kyushu. J. Japanese Soc. Grassl. Sci. 30:434-440.

National Animal Husbandry Research Station Annual Report from Naivasha, Kenya. 1979. Annual Report of the Scientific Research Division 1975. Ministry of Agriculture Research Report. pp. 162-178.

Nieto, F.G. 1985. Eragrostis curvula; a new grass for the Spanish flora. Anales del Jardin Botanica de Madrid. 42:255.

Novosad, A.C., D.J. Dorsett, G.W. Sultemeier, F.C. Petr, and J.N. Pratt 1973. Weeping lovegrass. Texas Agr. Ext. Serv. Leaflet 1207

Oquendo, G., J. Gerardo, and E. Mantecon 1983. Performance of pasture cultivars on brown soils in Guaimaro. Pastos and Forrajes 6:319-329. [In Spanish]

Palmer, W.C. 1964. Meteorological drought. USDA- Weather Bureau, Res. Pap. No. 45. Washington, D.C.

Pitman, W.D., D.M. Victor, and E.C. Holt 1981. Digestibility of kleingrass forage grown under moisture stress. Crop Sci. 21:951-953.

Pitman, W.D. and E.C. Holt 1983. Herbage production and quality of grasses with livestock and wildlife values in Texas. J. Range Manage. 36:52-54.

Pratt, J.M., A.C. Novosad, K.E. Lindsey, D.A. Lovelace, R.B. Metzer and F.C. Petr 1971. Keys to profitable permanent pasture production in west Texas. Texas Agr. Ext. Ser. MP-981.

Read, J.C., B.J. Simpson and L.J. Streetman 1980. Registration of Renner weeping lovegrass. Crop Sci. 20:670.

Rees, M.C. 1972. Winter and summer growth of pasture species in a high rainfall area of southeastern Queensland. Trop. Grassl. 6:45-54.

Reis, P.R., W. Botelho, L.A.S. Melo, and J. Kakida 1984. Pasture froghoppers (Sulia entreriana) in the north of Minas Geruis State, Brazil. Anais de Sociedada Entomologica de Brazil 13:225-236. [In Portuguese]

Rethman, N.F.G. and C.C. De Witt 1984. The production potential of pure and mixed stands of Eragrostis curvuala and Medicago sativa on the eastern Transvaal highland. J. Grassl. Soc. sth. Afr. 1:30-32.

Rodel, M.G.W. 1972. Effects of different grasses on the incidence of neonatal goitre and skeletal deformities in autumn born lambs. Rhodesia (Zimbabwe) Agr. J. 69:59-60.

Rodel, M.G.W., J.A. Shepherd, and G. Scheerhoorn 1976. Effects of plant parasitic nematodes on growth of grasses. p. 114-115. In Annual Report, Henderson Res. Sta., Salisbury, Rhodesia (currently Harrie, Zimbabwe).

Rodel, M.G.W., J.N. Boultwood, and L. McNeill 1981. The response of four grasses to applied nitrogen in two soils. Zimbabwe J. Agr. Res. 19:7-49.

Rodel, M.G.W. and J.N. Boultwood 1981. Effects of defoliation frequency on yield and composition of shoots and roots of three grasses of different growth habits. Zimbabwe J. Agr. Res. 19:151-162.

Rommann, L.M. and W.E. McMurphy 1974. Weeping lovegrass. Oklahoma State University Ext. Facts No. 2556.

Sanchez, A. 1976. The production of Lehmann lovegrass in Chihuahua. Pastizales 7:2-8. [In Spanish]

Sellers, W.D. and R.D. Hill 1974. Arizona climate. Univ. of Arizona Press, Tucson.

Shoop, M.C. and E.H. McIlvain 1970. Winter grazing of weeping lovegrass in northern Oklahoma. p. 122-129. In R.L. Dalrymple (ed.). Proc. Weeping lovegrass symposium. Samuel Roberts Noble Foundation, Ardmore, Oklahoma.

Shoop, M., E.H. McIlvain, and P.W. Voigt 1976. Morpa weeping lovegrass produces more beef. J. Range Manage. 29:101-103.

Stubbendieck, J., P.T. Koshi and W.G. McCully 1973. Establishment and growth of selected grasses. J. Range Manage. 26:39-41.

Stubbendieck, J. 1974. Effect of pH on germination of three grass species. J. Range Manage. 27:78-79.

Sweeney, F.C. and J.M. Hopkinson 1975. Vegetative growth of nineteen tropical and semi-tropical pasture grasses and legumes in relation to temperature. Trop. Grassl. 9:209-217.

Taliaferro, C.M., R.M. Ahring and W.L. Richardson 1983. Registration of OKPC-1 Kleingrass germplasm. Crop Sci. 23:190.

Thornber, J.J. 1905. Range improvement. Arizona Agr. Exp. Sta. 16:17-22.

Tischler, C.H. and P.W. Voigt 1983. Effect of planting depth on vegetative characteristics of three forage grasses at 14 days post emergence. Crop Sci. 23:481-484.

Van den Berg, E. 1985. Notes on the genus *Afrina brzeski*, 1981 (Anguinidae:Nematoda) with descriptions of new and known species. Phytophylactica 17:67-79.

Van der Merwe, W.J.J., A. Eicker, W.F.O. Marosas and T.S. Kellerman 1979. Aerospora of an *Eragrostis curvula* pasture in South Africa. Onderstepoort J. Vet. Res. 46:19-25. [In Afrikaans]

Voigt, P.W. 1971. Registration of Morpa weeping lovegrass. Crop Sci. 11:312-313.

Voigt, P.W., C.L. Dewald, J.E. Matocha, and C.D. Foy 1982. Adaptation of iron - efficient and inefficient lovegrass strains to calcareous soils. Crop Sci. 22:672-676.

Wang, H.T., S.M. Chang, C.W. Cheng and C.S. Chang 1975. Observations on cover crops and mulching on a steeply sloping orchard. J. Agr. Assoc. China 1:69-76.

Watt, L.A. 1976. Evaluation of pasture species for soil conservation on cracking black clays - Gwydir district, northwestern New South Wales. J. Soil and Water Cons. (New South Wales) 32:86-97.

Watt, L.A. 1983. Improving grass seedling establishment on black earths. J. Soil and Water Cons. (New South Wales) 39:201-207.

Winkworth, R.E. 1963. The germination of buffelgrass (*Cenchrus ciliaris*) seed after burial in a Central Australian soil. Aust. J. Exp. Agr. and Animal Husb. 3:326.

THE DISTRIBUTION, GROWTH CHARACTERISTICS, AND UTILIZATION OF LEHMANN LOVEGRASS IN SOUTHERN AFRICA

Jan H. Fourie[1] and Jerry R. Cox[2]

ABSTRACT

Lehmann lovegrass (Eragrostis lehmanniana) a subclimax, perennial, warm-season bunchgrass is native to the semiarid lands along the eastern Kalahari Desert boundary in southern Africa. This grass easily reestablishes after drought and is less palatable than other climax grasses. Selective animal grazing increases the opportunity for Lehmann lovegrass to spread and occupy overgrazed areas.

INTRODUCTION

Within the Kalahari Desert interior, in southern Africa, soils are deep sands, shrubs are widely spaced, and annual rainfall is usually less than 200 mm. Along the eastern Kalahari boundary (central Namibia, southwestern Botswana, and central South Africa), however, fine soil particles increase, grass and shrub densities increase, and annual precipitation exceeds 250 mm (Fourie and Roberts 1976). In these semiarid areas Lehmann lovegrass (Eragrostis lehmanniana), a perennial, warm-season bunchgrass is often the predominant forage species.

Along the eastern Kalahari Desert boundary, the forage produced in dry or drought years is not great enough to support domestic grazing animals because stocking rates are based upon forage produced in years when rainfall is above-average. During drought and overgrazing, perennial grass vigor declines and preferred climax grasses, as well as Lehmann lovegrass, often die. When soil moisture conditions improve, however, Lehmann lovegrass reoccupies void sites because it is a prolific seed producer (Fourie and Roberts 1977). Hence, the distribution of Lehmann lovegrass is increasing while preferred climax grasses are decreasing.

As Lehmann lovegrass densities increase, its importance in animals' diet should increase. Therefore, ecological studies are needed to determine how Lehmann lovegrass responds to climate when plants are found on different soil types, and grazing studies are needed to evaluate management strategies and stocking rate effects on plant production.

METHODS

Experiment I. The influence of elevation, soil type, temperature and precipitation on Lehmann lovegrass colonization:

Eight sites were selected in southern Africa where Lehmann lovegrass was the predominant forage grass. Site selection was based upon (1) whether Lehmann lovegrass actively colonized disturbed areas, (2) persisted, but did not colonize disturbed areas, and (3) the availability of long-term monthly precipitation and temperature records. Climatic data were summarized by month in the following categories: (1) mean maximum temperature, (2) mean minimum temperature, and (3) precipitation.

Experiment II. Seasonal dry matter production and digestibility of Lehmann lovegrass on three soil types:

Surface soils are sandy in the eastern Kalahari Desert, but surface soils may be underlain by either sand or layers of caliche ($CaCO_3$) and dolomite ($Mg(CO_3)_2$). An area where each soil type prevailed was excluded from grazing, and m^2 plots harvested at the soil surface during spring, summer and fall. Green forage collected at biweekly intervals was oven dried at 90° C, weighed, and converted to digestible organic matter (% DOM) using an in vitro technique (Tilly and Terry 1963).

Experiment III. The influence of two grazing strategies and three stocking rates on plant and animal production:

A 1,000 ha area at Armoedsvlakte Research Station was divided into six pastures, and three pastures were subdivided into six 30 ha paddocks. Large pastures were continuously grazed at light, medium and heavy stocking rates (Table 1) while subdivided pastures were rotationally grazed at light, medium and heavy stocking rates between 1977 and 1981. Animal numbers at the same stocking rate were similar in the continuously- and rotationally-grazed pastures, but animals were moved into a new paddock every seven days in the rotationally-grazed pastures. Equal numbers of Bonsmara steers (1 to 2 years old) were weighed when the study began and at completion in each of the four sampling years.

Table 1. Grazing management strategies and stocking rates at Armoedsvlakte Research Station, Northern Cape Region, South Africa.

Management Strategies	Stocking Rates (ha/Animal Unit)
Continuous Grazing	9.6 (light)
Continuous Grazing	7.0 (medium)
Continuous Grazing	4.0 (heavy)
Rotational Grazing	9.7 (light)
Rotational Grazing	7.1 (medium)
Rotational Grazing	4.1 (heavy)

[1]Manager, Division of Agric. Development, Sentraalwes, Bloemfontein, South Africa
[2]Range Scientist, USDA-ARS, Aridland Watershed Management Research Unit, 2000 E. Allen Road, Tucson, AZ 85719

Basal cover of individual grass species was measured in each pasture and paddock prior to grazing and at six week intervals during active plant growth. Animal utilization was estimated for each grass species using the following formula:

$$\text{Botanical Diet Composition} = \frac{(a \times b)}{\text{Total } (a \times b) \text{ of all species}}$$

Where:
    a = average frequency of the utilized species

    b = botanical composition of individual species

Prior to and during grazing the standing crop of each species was determined in each pasture or paddock. Green forage was separated from dry forage, and both were dried at 70° C for 24 hours. Each forage component was ground over a 1 mm screen, and samples analyzed to determine crude protein and in vitro digestibility (Fourie, et al. 1985).

RESULTS

Experiment I

In the semiarid Kalahari Desert area Lehmann lovegrass is found at elevations ranging from 800 to 1,700 m, and where annual precipitation amounts vary from 180 to 630 mm. Surface soils are always sandy and sometimes covered with gravel. Sandy surface soils may be underlain with deep sand or shallow layers of caliche and dolomite (Fourie and Roberts 1976). Mean monthly maximum and minimum temperature extremes vary from 35 to 15° C and from 0 to 20° C in summer and winter, respectively.

Dense Lehmann lovegrass stands often occur along the eastern Kalahari boundary (see dark line in figure 1), and only in these areas does the species actively colonize disturbed sites (Sites 1, 2, 3 and 4). The species occurs, but does not actively colonize disturbed sites to the west and south where annual precipitation varies from 180 to 270 mm (Sites 5 and 6) or to the east where annual precipitation varies from 550 to 630 mm (Sites 7 and 8).
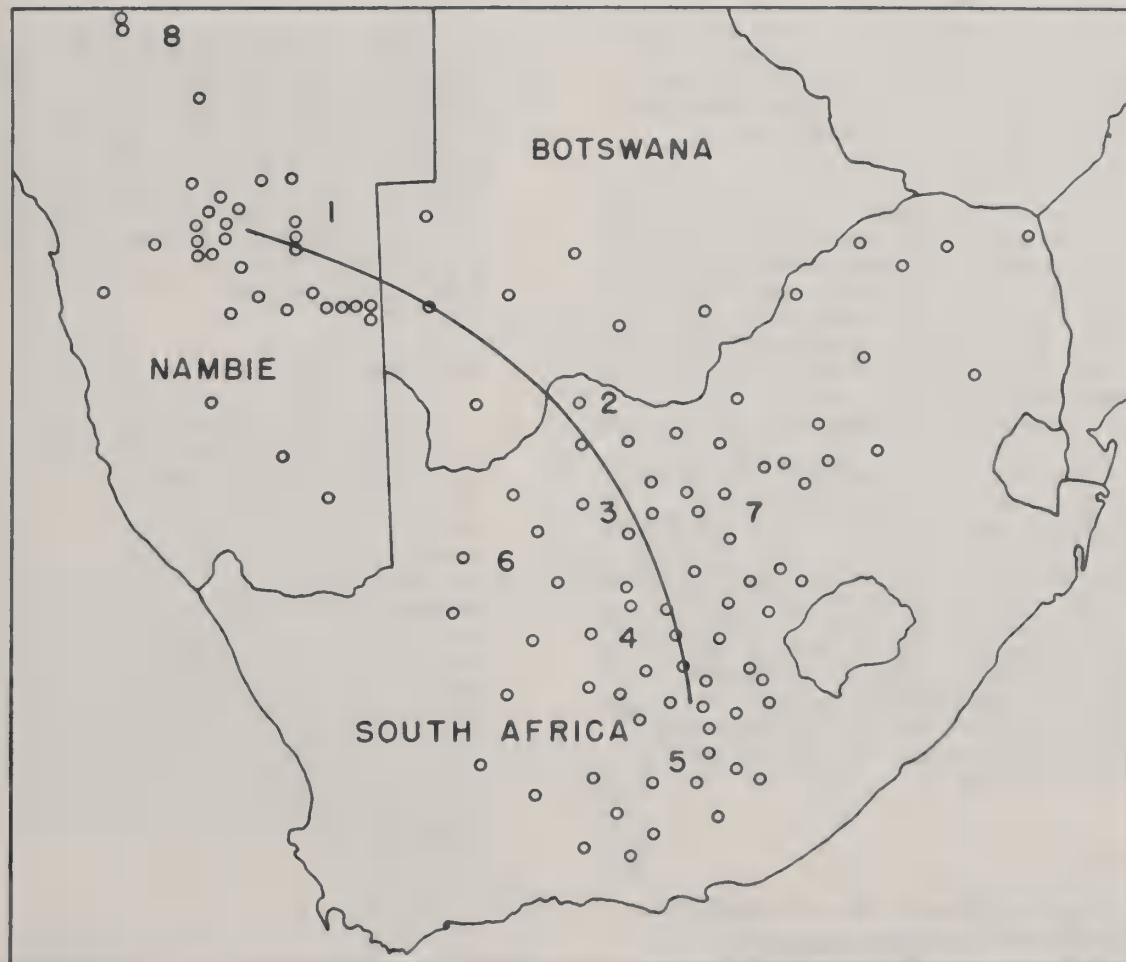

Figure 1. The Distribution of Lehmann Lovegrass in Southern Africa.

The amount and distribution of summer rainfall apparently determines the abundance of Lehmann lovegrass (Cox and Ruyle 1986). Where the species actively spreads in southern Africa growth occurs in spring and summer, but peak production immediately follows a series of summer storms that deposit approximately 140 mm in 30 to 45 days (figure 1; Sites 1, 2, 3 and 4). Lehmann lovegrass frequently dies during mid-summer droughts at Sites 5 and 6, but it reestablishes from seed when soil moisture conditions improve, or fails to compete with more robust grasses at Sites 7 and 8 where summer rainfall exceeds 300 mm.

Experiment II

Lehmann lovegrass initiates growth as temperatures warm in spring, but peak production amounts are dependent upon the amount and distribution of precipitation and sand depth (Fourie and Roberts 1977). Lehmann lovegrass stands growing in deep sands may produce 1,260 kg/ha if light, but frequent showers occur in spring. While stands growing in shallow sand underlain by dolomite or caliche produce 150 and 330 kg/ha, respectively. When early summer droughts occur, stands growing in deep sands produce 560 kg/ha, but stands on shallow sands produce from 0 to 150 kg/ha. If late spring and early summer are dry, stands growing in shallow sand may die, but when soil moisture conditions improve in late summer, seed germinate and seedlings reoccupy the site.

Peak green forage production of Lehmann lovegrass growing in the three soils occurs in late summer (Fourie and Roberts 1977) when culms elongate (Fourie, et al. 1985). Green forage production is greatest from plants growing in deep sand (1,540 kg/ha) intermediate from plants growing in shallow sand underlain by caliche (900 kg/ha) and least from plants growing in shallow sand underlain by dolomite (250 kg/ha).

The digestible organic matter (DOM) of Lehamnn lovegrass growing in the three soil types averaged 48% in spring, 68% in summer and 36% in fall; and was substantially less than other climax grasses (Fourie and Roberts 1977). DOM of plants growing in the three soil types was similar in spring and fall, but greater in summer from plants growing in shallow sand underlain by dolomite. Lehmann lovegrass seedlings that reoccupied the dolomite soil type were smaller and less fibrous than surviving mature plants on deep sand and shallow sand underlain by caliche.

Experiment III

Steers selectively grazed the palatable climax grasses; such as Chrysopogon serrulatus, Sporobolus fimbriatus, Themedia triandra, Digitaria seriata and Cymbopogon plurinodis and avoided Lehmann lovegrass. This trend occurred in all pastures and was not influenced by grazing strategy or stocking rate (Fourie, et al. 1986).

It was difficult for steers to consume the small basal Lehmann lovegrass leaves in spring, and they refused to graze the rapidly growing culms in summer (Fourie, et al. 1984). Animals preferred the large basal leaves and culm leaves produced by climax grasses.

The basal area and botanical composition of climax grasses and Lehmann lovegrass declined at all stocking rates in the continuously-grazed pastures an at the high stocking rate in the rotationally-grazed pasture (Fourie, et al. 1984). Mean daily animal gains were similar in the two grazing strategies and increased as stocking rates decreased (Fourie, et al. 1986). While forage quality was usually superior in highly grazed pastures (Fourie, et al. 1985).

Forage intake increased as stocking rates decreased, and there were no differences between the two grazing strategies (Fourie, et al. 1986). Forage intake in spring, summer and fall did not differ between the two grazing strategies when stocking rates were the same. In winter, however, steers in the continuously-grazed pastures consumed less forage, gained less weight and spent longer searching for forage than steers in the rotationally-grazed pastures.

The vigor of climax grasses declined in all pastures between year one and four, while Lehmann lovegrass production increased; the exceptions were the heavily-grazed pastures of both grazing strategies (Fourie, et al. 1985). The crude protein and digestibility of Lehmann lovegrass standing crop annually varied from 2 to 13% and from 40 to 69%, respectively. The crude protein and digestibility amounts measured for climax grasses were usually greater than those measured for Lehmann lovegrass.

DISCUSSION

In southern Africa (Fourie, et al. 1985), southeastern Arizona and northern Mexico (Cox and Ruyle 1986) Lehmann lovegrass initiates growth earlier than other climax grasses. Early growth in this instance does not necessarily imply animal use because leaves are difficult to graze. Grazing animals selectively graze other grasses because the quantity and quality of Lehmann lovegrass forage is less desirable. Grazing preference reduces the vigor of climax grasses and densities decline. This action increases the opportunity for Lehmann lovegrass to spread and colonize new sites. Since animal selectivity is the primary factor influencing the colonization of Lehmann lovegrass it seems likely that the grass will spread regardless of grazing stragegies and stocking rates.

LITERATURE CITED

Cox, J.R., and G.B. Ruyle. 1986. Influence of climatic and edaphic factors on the distribution of Eragrostis lehmanniana Nees in Arizona, USA. J. Grassl. Soc. Sth. Afr. 3:25-29.

Fourie, J.H., and B.R. Roberts. 1976. A comparative study of three veld types of the Northern Cape: Species evaluation and yield. Proc. Grassl. Soc. Sth. Afr. 11:79-85.

Fourie, J.H., and B.R. Roberts. 1977. Seasonal dry matter production and digestibility of Themada triandra and Eragrostis lehmanniana. Agroplantae 9:125-133.

Fourie, J.H., G.J. Redelinghuys, and D.P.J. Opperman. 1984. Influence of stocking rate and grazing system on plant basal cover and botanical composition of veld in the Northern Cape. J. Grassl. Soc. Sth. Afr. 1:20-24.

Fourie, J.H., D.P.J. Opperman, and B.R. Roberts. 1985. Evaluation of grazing potential of grass species in the Northern Cape. J. Grassl. Soc. Sth. Afr. 18-25.

Fourie, J.H., E.A.N. Engels, and B.R. Roberts. 1986. Herbage intake by cattle on Tarchonanthus veld in the Northern Cape as affected by stocking rate and grazing system. J. Grassl. Soc. Sth. Afr. 3:85-59.

Tilley, J.M.A. and R.A. Terry. 1963. A two-slate technique for the in vitro digestion of forage crops. J. Br. Grassl. Soc. 18, No. 2.

RANGE SEEDING RESEARCH IN NORTHERN MEXICO

Jorge Galo Medina T.[1] and Hector Garza C.[2]

ABSTRACT

The principles and practices of seeding arid rangelands in the central and southeastern portion of the Chihuahuan Desert in Mexico for the last 15 years are reviewed. Results have been highly variable as yearly rainfall fluctuated significantly over the time. Experimental evidences indicate that microtopographical soil surface modifications are necessary for successful seeding.

INTRODUCTION

Arid and semiarid lands in the Chihuahuan Desert of Mexico cover about two-fifths of the country's total land surface. Rangelands are a basic natural resource and the most important wild land use alternative. They support more than 16 million head of cattle, goats, sheep and horses (Medina, et al. 1985). Continuous yearly overgrazing and land plowing for rainfed crop farming have combined to convert a large proportion of range environs into low productivity areas. Present landscape is characterized by extensive bareground and dense invasions of less desirable forbs and woody species (Gonzalez and Fierro, 1985). It has been estimated that for improving the conditions of 37.5 million ha of degraded rangelands in the region artificial seeding is needed (Martinez and Maldonado, 1973).

A list of major problems depicting the situation of northern Mexico's natural resources include: 1) low levels of technology, 2) low levels of productivity, 3) overstocking, 4) weak efforts at range and livestock improvements, and 5) incipient attempts at range management research. Range research activities were formally initiated in 1957 at the short-grass and bunch-grass rangeland types in central Chihuahua. In 1962, the "La Sauceda" Range-Forestry Experiment Station was established in southeastern Coahuila (De La Cruz and Zapien, 1974). In 1971, the University Antonio Narro inaugurated an Aridland Research and Development Center, for a regional network of Experiment Stations (CNIZA, 1975).

Extensive studies have been conducted in the area focusing on the development of improved practices for transforming deteriorated ranges into more productive ecosystems. With regard to the revegetation practices, a common approach widely used is the strip farm seeding method. In addition, some other soil surface modification practices were developed to provide efficient range revegetation alternatives.

This paper is aimed to discuss the experimental works on range seeding carried out at the University Antonio Narro, ca., 1972-1986. It introduces current researchers with many unknown range seeding experiments commonly reported in interim papers. Obscure local publications and B.S. and M.S. thesis. Oftentimes, this information is not readily obtainable for most range scientists. Range seeding is regarded as one of the most advanced research topics in northern Mexico during the last twenty years (Fierro, 1974).

MATERIALS AND METHODS

Description of the Study Area

The study area is located in the southeastern and central portion of the Chihuahuan Desert. It lies within the north latitude belt of $23^\circ 40'$ to $27^\circ 36'$ and west longitude $100^\circ 45'$ to $103^\circ 45'$. The elevation ranges from 1200 to 1600 m. Topography consists mainly of alluvial soils, fans, extended pediments (1-4% slope), gentle-sloping hills and bottomlands. Parent material is primarily limestones. Soils are usually shallow with a caliche layer at a 10-40 cm depth. Annual precipitation varies from 250 to 400 mm, with about 60% distributed in summer (June-September). The average annual temperature ranges from 10° to 16° C.

The vegetation is characteristic of the desert scrub type. Primary vegetation types are the microphyllous desertic brushwood and the rosettophyllous desertic brushwood (Medellin-Leal, 1982; De La Cruz, et al. 1972). The shrub stratum is dominated by creosotebush (Larrea tridentata D.C.), tarbush (Flourensia cernua D.C.), mesquite (Prosopis spp), four-wing slatbush (Atriplex canescens Pursh), pricklypear cacti (Opuntia spp), palma (Yucca filifera) and ocotillo (Fouquieria splendens Engelm.). Herb vegetation consists of scattered grasses including green sprangletop (Leptochloa dubia H.B.K.), Arizona cottongrass (Digitaria californica Benth.), curly mesquite (Hilaria belangeri Steud.), plains bristlegrass (Setaria macrostachya H.B.K.), alkali sacaton (Sporobolus airoides Torr.), curly grama (Bouteloua breviseta Vasey), and many other annuals.

[1]Professor, Department of Renewable Natural Resources, Universidad Autonoma Agraria Antonio Narro, Saltillo, Coahuila 25315, MEXICO

[2]Coordinator, Animal Science Division, Universidad Autonoma Agraria Antonio Narro, Saltillo, Coahuila, 25315, MEXICO

Planting sites are found at the University Antonio Narro's Aridland Experiment Stations located in northwestern San Luis Potosi (Matehuala site), northeastern Zacatecas (Noria de Guadalupe site), northwestern Coahuila (Ocampo site) and northeastern Durango (Cuencame site). A brief description of each site follows.

The Matehuala station is located 3 km south of Matehuala, San Luis Potosi. Elevation is 1581 m and has a climate hot in summer and temperate during winter. Mean annual temperature oscillates from 18° to 22° C.; annual rainfall is about 440 mm with a summer dominance. Soils are primarily loams and clayey-loam, poor in organic matter and nitrogen. The Cuencame Station is located 19 km north of Cuencame, Durango. Elevation is 1665 m with a very dry desertic climate. Mean annual temperature ranges from 10° to 20° C. and average rainfall is 352 mm per year. Soils are loamy and clayey-loam. The Noria de Guadalupe Station lies 20 km south of Concepcion Del Oro, Zacatecas. Elevations range from 1780 to 1850 m. Climate is dry with an annual temperature ranging from 18° to 22° C. and an average precipitation of 350 mm. Soils are medium-textured with a low content of organic matter. The Ocampo Station is located 32 km north of Ocampo, Coahuila, at an elevation of 1200 m. Climate is hot and very dry, with an average rainfall of 275 mm. Soils are deep, sand-loams, clay-loams and lime-loams.

Experimental Procedures

A wide variety of seedbed practices have been evaluated. A guiding principle of most works is to harvest "in situ" rainfall to improve establishment and production of seeding. In order to present an overview of more significant works, they are classified into three groups: 1) strip farming methods, 2) pitting structures, and 3) microwatersheds.

Contour Strip Farming

The strip farming approach to range seeding is based on the principle of making "in situ" use of the runoff as it is collected from individual rainfall events. A series of terraces or berms, of variable width, are constructed along the contour. They include a catchment or runoff producing area--and a crop growing or runoff collecting sector (fig. 1) (Medina, 1976). Individual and mixtures of grasses have been planted. Most commonly used species are: buffelgrass (Cenchrus ciliaris), lehmann lovegrass (Eragrostis lehmanniana), green sprangletop, almum grass (Sorghum almum), sideoats grama (B. curtipendula), blue grama (B. gracilis), and four-wing saltbush. Strip farming systems have been studied from two perspectives: a) having the seedbed size
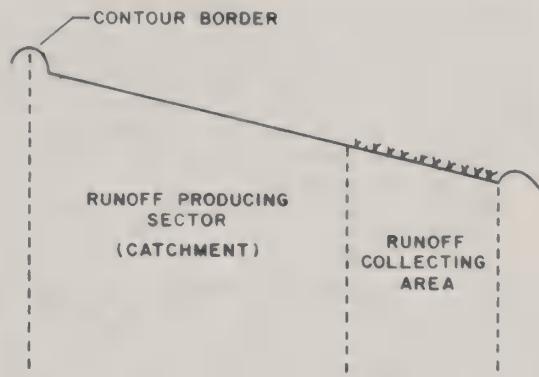

Figure 1. Graphical sketch of the desert strip farming method.

constant, while modifying the width of the catchment area; and b) having the catchment size constant, and modifying the width of the seedbed sector.

Pitting Structures

Pitting for range seeding is based on the principle of having a flexible seedbed in terms of soil moisture. It is assumed that within the pit three "microhabitats" are formed: a) a flooding section, b) an intermediate or mesic section, and c) an upper, dry or xeric section (fig. 2). In this manner it is possible to increase grass establishment, regardless of the precipitation amount occurring during the seeding season. Different shape and size of pits have been evaluated. Common shapes studied are: semicircular, semielliptic, and square. Pit sizes have ranged from 0.2 to 5 m^2. Both individual and mixtures of grasses and forbs have been tested.

Microwatersheds

Soil surface modification practices have been studied to increase the quantity of runoff water that can be harvested. A basic approach consists of constructing two-sided, V-shaped microwatersheds. The soil surface is graded to have slopes from 10 to 20% within the microwatershed. To uniformly distribute the water, microwatersheds are constructed along the contour. Their design is based on the same "microhabitat" principle of the pitting. Four soil-moisture positions within the microwatershed are identified: a) bottom, b) intermediate slope, c) upper slope and d) ridge (fig. 3).

It is assumed that in dry years, seedlings will emerge at the bottom sector of the microwatershed; low rainfall will only allow grass establishment at the lower part of the structure where some additional runoff may occur. For normal or average years, grass establishment will occur at the low and

intermediate sectors. During extreme wet years, the bottom and intermediate sections of the microwatershed will be flooded; thus seed will emerge at the intermediate and upper sectors. In the long run, microwatersheds are assumed to perform in accordance with the amount of rain falling during the seeding season.
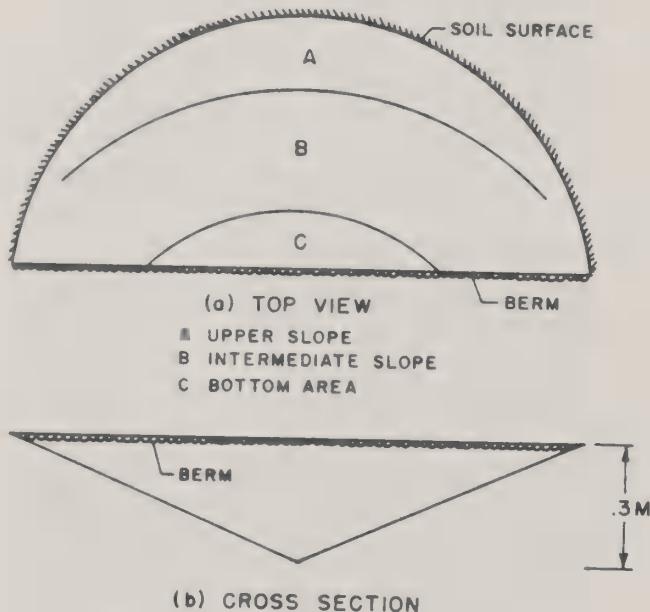

(a) TOP VIEW

A UPPER SLOPE
B INTERMEDIATE SLOPE
C BOTTOM AREA

(b) CROSS SECTION

Figure 2. Graphical representation of pitting structures.

Contour Strip Farming

Background

Early revegetation practices in the area are reported by De La Cruz and Zapien (1974). After ten years of observations at "La Sauceda" Range-Forest Station they concluded that the best method for increasing forage production by artificial revegetation was to alternate strips of native vegetation with forage-growing seedbeds, about ten m in width. Grasses evaluated included blue panic grass (Panicum antidotale), sideoats grama, buffel grass and rhodes grass (Chloris gayana). Reseeded strips increased production from 20 to 38 times more than the native vegetation. A major contribution to the success of these seeding trials was the additional runoff collected from the upper slopes. The authors recognized that seeding practices in the area should be confined to bottomlands where substantial amounts of runoff water can be channeled from upper sites. This recommendation was confirmed by Reynaga, et al. (1976) in a large-scale seeding trial on a 100 ha plateau exclosure dominated by creosotebush and tarbush. Five single species were planted: buffel grass, rhodes grass, blue panic grass, plains bristlegrass and almum sorghum in various seedbed preparation practices for a total of 20 different treatments. The experiment was located at a low-elevated plateau (meseta) that did not receive additional runoff from upper parts of the area. The study included 40 alternate strips (15 m width) of native
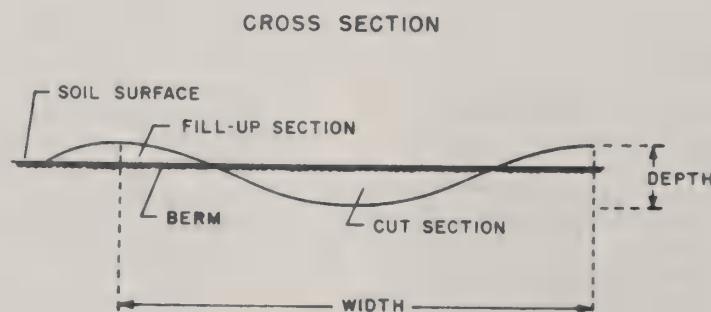
CROSS SECTION

Figure 3. Graphic representation of the two-sided microwatershed.

undisturbed vegetation (runoff producing sector) and prepared seedbeds (runoff collecting sector). Due to the low rainfall occuring during the growing season (84 mm), the overall establishment of grasses was less than 3%. No water yield from the catchment areas was observed. Establishment of species occurred primarily in the natural depressions or micro-basins of seedbeds. In practical terms, forage yield and establishment of the whole experiment depended only on the direct rain that fell on seedbeds. It was concluded that a successful seeding by alternate strip farming is dependent on either higher precipitation conditions or additional runoff water to the seedbed from upper places. A complementary study was carried out in the same area, on a lowland, deep alluvial soil. Seeding of sideoats grama and rhodes grass were compared to a series of manual, selective shrub removal practices, on a ten-year exclosure (Mellado, et al. 1976). The best treatment was a sideoats grama seeding yielding 2379 kg/ha dry matter. This result showed the important role of selecting a proper seeding site. A combination of good soil conditions and high potential for runoff concentration are two key aspects to increase forage production in arid shrubgrass sites.

Matehuala Site

Munoz and Castro (1974a) describe the performance of a strip farming seeding system with three seedbed area. Catchment area ratios were 1:1.5, 1:4, and 1:9. The effect of the catchment sector was studied in two conditions: undisturbed native vegetation and cleared. A mixture of forage species was planted including buffel grass, rhodes grass and four-wing saltbush. The authors concluded that in years with above normal rainfall amount, the size of the runoff catchment area were not significantly different (p <.05). For normal or below-average rainfall years, there exists a marked difference amount runoff producing sector sizes. Forage yield per seeded unit area (m^2) increases as the runoff sector strip becomes wider.

The effect of proper topographical surveying during construction of contour level borders in strip farming systems was evaluated by Munoz and Castro (1974b). A mixture of buffel, lehmann lovegrass and rhodes grasses was planted to evaluate establishment and forage yield as indicators of strip farming systems performance. When microtopography was considered in construction of the borders (berms) along the contour, establishment and forage yield of seeded grasses was higher than with the traditional method (construction of terraces parallel to base contour lines). Another runoff collected was more uniformly distributed in the crop growing area. However, the results were not significantly different.

Noria De Guadalupe Site

Rodriguez, et al. (1976) compared five alternatives to improve range productivity on a creosotebush/tarbush range site. They were: a) contour borders, b) seeding with an animal-draft plowing, c) seeding with a tractor discing, d) seeding after manual shrub removal and tractor discing, and e) undisturbed native range. They planted a mixture of sideoats grama, buffel grass, almum grass, green sprangletop and lehmann lovegrass. During a three-year evaluation period, forage yield varied considerably from season to season. In the first growing season, highest yield was observed in the seeding treatment with brush removal (434 kg/ha, DM). In the second year, the tractor discing seedbed resulted in the highest forage yield (55 kg/ha, DM). At the third year, best treatment was the animal traction plough-prepared seedbed (207 kg/ha, DM). The variable results were attributed to the highly fluctuating precipitation conditions. For the range of alternatives evaluated, the authors concluded that the best alternative to restore degraded rangelands in the area was the rest of undisturbed native vegetation.

Aguirre, et al. (1976) conducted a seeding experiment by using two methods for collecting "in situ" runoff water: a) traditional strip farming in 20 m width terraces (a 3 m width seedbed and 17 m width catchment), and b) a modified strip farming with a micro-seedbed, triangle-shaped constructed along the contour level terrace, with the same runoff producing sector than above. The micro-seedbed was partially planted in four proportions of the total area: 16.7%, 9.4%, 4.2% and 1.04%, to a mixture of sideoats grama, rhodes grass, almum sorgum and four-wing saltbush. After a three-year period evaluation, it was concluded that there existed a direct relation between the size of planted area and forage yield; as the runoff producing sector is increased, forage yield per seeded unit area decreases; conversely, as the cropped or planted area increases, runoff water is more efficiently used to produce grass forage. Similar results were obtained by Nava, et al. (1977). They studied a wider range of cropped area to catchment area ratios. Cropped area varied from 1 to 50% of the total area (catchment included). They found that for regular and above-average rainfall conditions, desert strip farming systems with a low proportion of crop growing area and a large catchment area tend to be most effective in the use of the available runoff water; however, for below-average rainfall conditions this tendency is reversed.

Cuencame Site

Strip farming treatments with seedbed area: catchment area ratios of 1:4, 1:7, and 1:10 were evaluated by Medina, et al. (1986). The study showed that annual rainfall conditions had a greater effect in forage production than the treatments involved. Forage yield varied more among years than among treatments. A restoration experiment involving eight seedbed practices is described by CNIZA (1975). They compared shrub removal with a root-cutter and hand grubbing, and a strip farming seedbed, 3 m width, prepared by hand and with a root-cutter. These seedbeds were planted before and after the rainfall season, with a mixture of the following grasses: almum grass, sideoats grama, lehmann lovegrass and green sprangletop. Forage yields expressed in g/m^2 were significantly different (p <.05); however, when forage yield was transformed to kg/ha, the results were inverted. The loss in production from the area used as a runoff catchment was not compensated by the increased forage yield expected on the seeded area. Considering the strip farming system as a whole (catchment area and crop growing area), it will require about 3.5 more surface area to produce the same amount of forage as from a conventional seeding work (total area seeded).

Ocampo Site

Gonzalez (1974) describes a strip farming seeding trial using three crop:catchment ratios: 1:3.75, 1:7.5 and 1:11.25. Almum sorghum was planted to a density of 12 kg/ha PLS. No significant difference was found among treatments. Although runoff was not quantitatively measured, the author observed that all treatments had an excess water from the catchment area. Four ratios of cropped area:catchment area (1:1, 1:1.3, 1:2 and 1:4) of the desert strip farming seeding method were studied by Garza, et al. (1977). A mixture of the following grasses was used: green sprangletop, sideoats grama, lehmann lovegrass, almum sorghum and rhode grass. At the end of a four-year evaluation, the 1:1.33 seedbed:catchment ratio had a yield of 2300 kg/ha (DM) (Garza, et al. 1978). In spite of the striking results obtained by the strip farming method, the authors observed that this approach shows a highly unstable production through time. There was a tendency of increased forage yield as the seedbed width diminished. A large-scale seeding experiment was reported by Gloria, et al. (1978). They used a 200 ha creosotebush-tarbush range site to evaluate three seeding treatments: a) alternate strips of 2 m width seedbed and 8 m width catchment (undisturbed native vegetation), b) same treatment as above, but no borders or berms were erected in the seeded area, and c) alternate strips as in a), but not seeded. A drastic drought occurred in 1974, and the yield of seeded areas was nil. At the end of

1976, the strip farming area had a 25.5% establishment and a total yield of 1284 kg/ha (DM), while the control and unseeded strip had an average yield of 170 kg/ha (DM). This trial reconfirmed the high unstability in production of strip farming systems. The authors concluded that the strip farming may work in the area if either a) the slope of the runoff catchment area is increased to effectively induce runoff, or b) the rainfall randomness is reduced and its amount increased. Flores (1980) compared a strip farming 1:2 seedbed:catchment ratio to other seedbed treatments. The study shows that this method is less effective in terms of establishment and yield than the pits and microwatersheds.

Rodriguez (1980) compared strip farming seeding to several selective shrub removal treatments at an alkali sacaton, saline bottomland range site. For a five-year evaluation period, seeding performance was less than the undisturbed native range vegetation in terms of forage production. The author concluded that for these sites, range manipulation through shrub control restoration practices are more effective than seeding. Galicia (1980) studied the widest possible gamut of seedbed:catchment ratios, on strip farming. One set of treatments consisted of constant catchment strips width constant, and variable seedbed widths: 4:1, 2:4, 4:4, 8:4, 12:4, 24:4, and 36:4. Another set of treatments included a constant seedbed strip sector and variable catchment widths: 4:0, 4:1, 4:4, 4:8, 4:12, 4:24, 4:36, and 4:48. In this way, 15 ratios ranging from 1:0.25 to 1:12 were considered in this study (seedbed:catchment). A mixture of the following grasses were "seeded"; almum grass, lehmann lovegrass, blue grama, sideoats grama, and green sprangletop. In the first growing season (251 mm of rainfall) the best treatments were the 1:6 and 1:9 ratios with a yield of 72 and 173 kg/ha (DM) respectively. In the second year (341 mm of rainfall) all treatments showed significant differences in forage yield. Best ratios were 1:12 and 1:9 with 193 and 163 kg/ha (DM) respectively. The lowest rainfall conditions (180 mm) occurred affected all treatments. Best yield responses were the ratios 1:3 and 1:12 for a 77 and 40 kg/ha (DM) yield, each. This study also confirmed the unpredictible performance of desert strip farming systems. It failed to predict a reasonable tendency for using a particular range of ratios for specific rainfall conditions. This perhaps, is one area of research that has to be more carefully analyzed in the future.

In contrast, Garza, et. al. (1985) report a study of a ratio of 1:2 for the establishment of two native important grasses: blue grama and sideoats grama. Three seeding ratios were evaluated for each species: 8, 10 and 12 kg/ha PLS for sideoats and 4, 6, and 8 kg/ha PLS for blue grama. For a five year period, sideoats grama yield response was

notably high for all seeding rates; resulting for the 12 kg/ha seeding rate an overall average yield of 2298 kg/ha (DM). The response of blue grama was much more inferior for the same time span yielded an average of 802 kg/ha (DM) for a 8 kg/ha seeding rate.

Pitting Structures

Ocampo Site

Four combinations of pit size and shape were evaluated by Garza, et. al. (1977, 1982): semicircular 1.8 x 3.6 m, semielliptical 1.8 x 1.8 m, semielliptical 0.9 x 1.8 m, and square 1.8 x 3.6 m. Plots were seeded to a grass mixture at a rate of 16.2 kg/ha. For all pits, about 48% of seedling density was found in the bottom and about 10% in the upper slope. Adjusting the yield per unit seeded to kg/ha, semicircular pit resulted in the best treatment with a yield of 415 kg/ha. In comparison with the traditional strip farming systems, pits show important features and advantages. During years with below-average rainfall, the bottom section of pits collects enough water that provides for grass establishment that otherwise could not occur. In above-normal wet years, small pits showed better results, mainly because they are not flooded and water tends to distribute more uniformly. The semicircle shaped 3.6 x 1.8 m. pit was evaluated for the

establishment of sideoats and blue grama grasses. Seeding rates were 8, 10, and 12 kg/ha PLS for sideoats grama and 4, 6, and 9 kg/ha PLS for blue grama. For the overall period best treatments were 8 kg/ha seeding rate for sideoats grama (Table 1) and 8 kg/ha seeding rate for blue grama (Table 2).

Ibarra, et al. (1980) studied pits for the establishment of four-wing saltbush from seed. Five seeding densities on five pitting structures were evaluted. The seeds used in this work were collected in the general area and stored for a seven month period before seeding. Following mechanical scarification with a blender, the seed were direct seeded into seedbeds and covered with a light harrow of branches. Afterward, the pits were covered with native vegetation brush to provide a mulch. An inverse relationship between size of the pit and the seeding rate was found. For the large pits best responses were found with the lower seeding rates. The study showed the feasibility of direct seeding of a forage forb for range restoration. Highest plant densities and yield were found at the larger pits and higher seeding rates (Table 3).

Table 1. Yield (Dry matter) of Bouteloua Curtipendula in 3.6 m x 1.8 m pits. Ocampo Experimental Station. Coahuila, Mexico.

Seeding Rate	YEARS				
	1977	1978	1979	1980	1981
kg/ha	----------------g/m^2--------------------				
8	0	118.85	212.00	152.14	1215.18
10	0	29.78	361.27	278.16	481.67
12	0	84.41	446.87	338.92	677.59

Table 2. Yield (Dry matter) of Bouteloua gracilis in 3.6 m x 1.8 m pits. Ocampo Experimental Station. Coahuila, Mexico.

Seeding rate	YEARS				
	1977	1978	1979	1980	1981
kg/ha	----------------g/m^2--------------------				
4	0	279.63	31.33	28.16	678.15
6	0	141.31	110.27	99.71	672.59
8	0	206.48	234.20	203.02	1050.45

Table 3. Density, height, vigor and production of _Atriplex canesce_ five
pit sizes. Ocampo Experiment Station. 1979. (Adapted from
Iberra, et al. 1980)

Treatment		Parameter			
Seedbed 1/ Structure	Seeding Structure	Density	Height	Vigor	Yield
S	(kg/ha)	(Individuals/m^2)	(cm)		(G/m^2, DM)
	D_1	0.20	3.5	4.3	6.88
	D_5	1.38	10.25	2.7	47.83
S_1	D_{10}	5.70	13.44	2.4	199.68
	D_{15}	5.10	9.68	1.9	176.56
	D_{20}	4.82	7.34	2.8	166.08
	D_1	0.20	3.5	4.5	6.89
	D_5	5.11	13.06	2.5	179.23
S_2	D_{10}	1.38	6.13	2.8	47.63
	D_{15}	4.13	10.44	2.6	142.97
	D_{20}	4.72	7.26	2.7	163.69
	D_1	0.79	3.25	4.3	27.32
	D_5	0.79	5.0	3.0	27.27
S_3	D_{10}	0.79	4.5	4.0	27.22
	D_{15}	3.93	11.25	2.7	136.26
	D_{20}	2.36	4.2	2.1	81.37
	D_1	0.79	2.0	4.5	27.20
	D_5	0.0	0.0	–	0.0
S_4	D_{10}	3.93	8.55	3.2	135.93
	D_{15}	3.93	7.0	3.3	135.71
	D_{20}	7.07	9.3	3.0	244.41
	D_1	0.0	0.0	–	0
	D_5	0.0	0.0	–	0
S_5	D_{10}	0.0	0.0	–	0
	D_{15}	0.0	0.0	–	0
	D_{20}	0.0	0.0	–	0

1/Structures

S_1 3.6 x 1.8 m semicircle
S_2 1.8 x 1.8 m semielipse
S_3 .9 x 1.8 m semielipse
S_4 .45 x 1.8 m semielipse
S_5 1.0 x 1.0 m control

* Arbitrary scale: 1 – Excellent
                    2 – Good
                    3 – Regular
                    4 – Poor
                    5 – Very Poor

Frias (1981) conducted a follow-up study in the same experimental layout to evaluate the performance of pits in time, with respect to emergence of seedlings, seedling vigor and growth. During a 19 month study period he found seedling emergence on control plots (flat smooth soil surfaces) from seeds that in past seasons had failed to germinate. Treatments with the highest seedling densities presented the highest rates of deaths. Most of the seedlings were established at the intermediate position of the pits. In general, four-wing saltbush seeds were active for two years following seeding. If unfavorable conditions are present, the seeds remain dormant until the proper conditions appear. For the overall study, the results indicate best responses are found with the treatments having a combination of large pits and high seeding rates.

Matehuala Site

Munoz and Elizondo (1974) carried out a seeding trial with rhodes grass in medium-sized pits, constructed with an eccentric tractor disc. Compared to contour furrowing, the pits were significantly different (p <.05). For the study conditions, pits preformed similar to seeding on flat, smooth surfaces; this is attributed to the extraordinarily high rainfall that occurred in the site (650 mm). With this high amount of moisture, pitting structures not needed for runoff water concentration.

Microwatersheds

Ocampo Site

Garza, et al. (1978, 1985) studied five combinations of slope and width of V-shaped two-sided microwatersheds: a) a 6 m width with 10% slope, b) 3 m width with 10% slope, c) 1.5 m width with 20% slope, d) 0.75 m width with a 20% slope, and e) .37 m width, 20% slope. Sampling was performed on four microtopographical positions within the microwatersheds: bottom, intermediate slope, upper slope, and ridge. For the first growing season, establishment occurred mostly at the bottom and lower slope sectors, and tended to diminish as upward the structure (Table 4). Seedling density varied directly proportional to the size of the microwatershed; higher densities are found at the larger microcatchments. With respect to forage yield, the same tendency was found, the more yield occurred at the bottom and lower slope sections (Table 5).

The 6 m wide treatment had a three-year average yield of 236 g/m^2. This is 30 times greater than control. When yield was adjusted to kg/ha, the treatment had a three-year average yield of 1173 kg/ha, fifteen times higher than control (Table 6).

Table 4. Grass density in relation to the micro-topographic position in different sizes of two-sided microwatershds.

Treatments[1]	Position on Microwatershed				Mean
	Bottom	Lower Slope	Upper Slope	Ridge	
(m)	----------------- individuals/m^2-----------------				
0.37	18	2	0	0	5
0.75	25	28	12	3	17
1.5	117	73	13	0	51
3.0	138	82	0	0	55
6.0	153	65	0	0	55

[1] Width of the two-sided microwatersheds.

Table 5. Mean forage yield (DM) for different sizes of two-sided micro-watersheds.

Treatments[1]	Position on microrelief[2]	Yield		
		1975	1976	1977
(m)		------------g/m^2------------		
Control	–	4.5	10.0	9.3
0.37	A	2.27	20.85	1
	B	1.24	0	1
0.75	A	27.12	27.83	40.0
	B	6.34	21.33	5.3
1.5	A	59.32	99.57	84.4
	B	1.1	13.75	15.4
3.0	A	76.32	114.9	267.3
	B	0	0	0
6.0	A	106.1	148.7	452.4
	B	0	0	0

[1]   Width of the two-sided microwatersheds.

[2]   A – Lower half section
       B – Upper half section

Table 6. Mean forage yield (DM) of a grass mixture seeded in two-sided micro-watershed.

Treatments[1]	Yield			
	1975	1976	1977	Average
	--------------------------kg/ha-------------------			
Control	50	100	93	81
0.37	20	103	10	44
0.75	162	246	226	211
1.5	300	566	498	455
3.0	380	574	1333	762
6.0	528	740	2252	1173

[1] Width of the two-sided microwatershed

In general, V-shaped microrelief structures showed inverse results than compared to pits. A direct relationship between size of treatment and yield per hectare was observed. Even though that treatments 1.5 m width or smaller presented a more uniform yield and plant establishment within the structure, their yields were the lowest ones. These treatments would become advantageous over the larger ones during above-average precipitation conditions, because of the better distribution of the rainfall within them. A factor that obviously has greatly contributed to the excellent performance of the two-sided microwatersheds is the slope, which was increased from 1% in natural conditions of the study site to 10 and 20%. Thus, more runoff is induced to the lower portions of microcatchments, resulting in more foliage growth and forage yield.

It is a common tenet in most range revegetation works that native grass species are more difficult to establish than the introduced ones. With this problem in mind, Garza, et al. (1982) evaluated the 3 and 6 m width microcatchments (two-sided) for establishing sideoats and blue grama grasses, under three seeding rates each. A 10 kg/ha PLS seeding rate for sideoats grama showed the best forage yield response in the 3 m width watershed (Table 7). Highest yield of blue grama for the same size of catchment was obtained at a seeding rate of 6 kg/ha PLS (Table 8). With regard to 6 m width catchments, the best response of sideoats grama was observed at the 10 kg/ha PLS rate for blue grama a seeding rate of 8 kg/ha produced the highest yield (Table 10). From this work, it is concluded that the V-shaped two-sided microcatchments do provide an excellent seedbed for establishing good quality native species under highly variable rainfall conditions. On the average, a trend was observed that forage yield increased in direct proportion to the size of the catchment.

Table 7. Yield (Dry matter) of Bouteloua Curtipendula in 3 m wide two-sided microwatersheds. Ocampo Experimental Station, Coahuila, Mexico.

Seeding rate	YEARS				
	1977	1978	1979	1980	1981
kg/ha	------------------g/m^2--------------------				
8	2.96	243.52	344.83	216.13	456.48
10	3.33	175.00	421.67	212.60	875.00
12	5.18	164.81	307.00	270.16	408.77

Table 8. Yield (Dry matter) of Bouteloua Curtipendula in 3 m wide two-sided microwatersheds. Ocampo Experimental Station, Coahuila, Mexico.

Seeding rate	YEARS				
	1977	1978	1979	1980	1981
kg/ha	----------------g/m^2--------------------				
4	16.68	127.78	230.07	189.17	215.74
6	4.11	51.85	351.73	331.22	282.41
8	15.22	65.74	217.97	197.18	280.55

Table 9. Yield (Dry mattergrams/m^2)) of Bouteloua Curtipendula in 6 m wide two-sided microwatersheds. Ocampo Experimental Station, Coahuila, Mexico.

Seeding rate	YEARS				
	1977	1978	1979	1980	1981
kg/ha	--------------------g/m^2----------------------				
8	76.78	309.78	167.07	120.18	846.29
10	6.22	176.85	208.40	127.18	916.20
12	17.89	392.59	387.70	306.92	396.75

Table 10. Yield (Dry mattergrams/m^2)) of Bouteloua Curtipendula in 6 m wide two-sided microwatersheds. Ocampo Experimental Station, Coahuila, Mexico.

Seeding rate	YEARS				
	1977	1978	1979	1980	1981
kg/ha	--------------------g/m^2----------------------				
4	21.66	179.17	235.47	200.14	496.75
6	48.67	183.80	88.33	72.30	451.38
8	12.67	134.26	221.63	137.14	596.29

SUMMARY AND CONCLUSIONS

From the wide array of ecological conditions in planting sites, seedbed preparation techniques and sown plant species during the last 15 years in the study area, it is difficult to assess specific recommended practices for particular range sites. The widely fluctuating precipitation observed over time throughout the area further complicates data analysis to draw meaningful conclusions. What have we learned from this experimental scenario? Can we provide ranchers and land producers with concrete, failure-proof improved practices for restoring degraded, low-productivity rangelands? What research areas seem to be missing for a more objective and integrative approach to range seeding? Experimental evidence provides us with more questions than answers.

Certainly, a successful seeding is not dependent on a single factor; a strong interaction exists among environment, seedbed conditions and range plants. For a given environmental site, none of the seedbed treatments under evaluation performed in a consistent fashion every time. Variable rainfall conditions override the beneficial effects of a seedbed practice found suitable for a particular site, and vice versa. Given the proper combination of environment and seedbed technique, the availability of good quality and range plants adapted to the area enters into consideration. Many of the large-scale seeding efforts that have failed in the past were not provided with the minimum, basic information about the quality properties of the seeds used: viability, germination percentage, etc. Few of the experimental trials have been documented in this regard.

Even though range seeding has an enormous potential for increasing forage production, the high costs and risks involved restrain its applicability in a broad scale. From our experience, range seeding must not be considered as an extensive, one-shot solution restoration alternative for deteriorated arid rangelands. It must solely be viewed within a total range management plant context. Regionally speaking, range seeding is indeed a viable ecological solution to prevent soil and water erosion for most range conservation purposes; however, at the local ranch level, its use and application will be dependent on a series of factors, including the past use history of land, present condition of the vegetation, available facilities (fencing, watering, etc.), range condition of the total area, and economic and financial situation of land owner. An important avenue of application of seeding practices at the ranch level is: a special-purpose pasture to serve as a flexible, stocking rate adjustment device for critical periods of management.

It will provide for a small-surface tract of high-yielding pasture that can aid in the implementation of a flexible range management plan and as an insurance or emergency crop for prolongated drought periods. Besides, an improved pasture can meet some complementary management objectives that in addition to making more forage available for grazing, it allows for specific areas to calving, weaning, cattle handling, cattle roundup for sanitary or selling purposes, and other routine ranching practices.

A large amount of data has been gathered in the area from the early 70's to date; however, some promising research areas can be pointed out for the near future. Native seed sources for commercial propagation do not exist at all for most valuable species. A native grass collection was started in the area at the time of the earliest seeding trials; however, seed production for large-scale revegetation works is still not available. Several promising cultivars or ecotypes of sideoats and blue grama have been developed that need further study in field conditions for seeding establishment and yield responses under an ample set of ecological conditions. In terms of range site environmental features, a series of local and regional studies are needed to characterize the agroecological requirements of native range plants that have proved to be important for seeding purposes. Little information from the area is available as relevant to restoration management of the land; in particular, we do not know the specific requirements for the germination, emergence, establishment, survival and full-cycle growth of species. Natural seeding ecology studies must form a parallel and closely tied research topic to artificial revegetation works. In order to match seeding results with climatological conditions for prediction and better understanding of seeding responses, a missing area of research is the development of a modeling approach to link the multiple intractions of environment (temperature and rainfall), seedbed (soil moisture conditions, runoff potential, catchment size, etc.) and plant growth (establishment and yield). An important question to answer is how often a particular set of agrometerological conditions observed for a given performance of seeding will replicate in the future, based on climatological records from the area. This will give a better panorama of the chances of having the same set of conditions for seeding establishment. Of course, a definitive test to successful seeding will be the utilization by grazing animals; grazing trials will have to be included as a part of the research activities of restoration.

Finally, with regard to the engineering aspects of seedbed preparation, much more work remains to be accomplished. On relatively flat areas, soil surface modification practices of altering the slope and microtopography of seedbed, have resulted into significant responses of plant yield. However, these methods are not available for practical applications from an economic perspective. In the end, seed and seedbed ecology and management research must be put into practical use by ranchers, livestock growers, and land producers. Seeding technologies must be ideally designed so as to meet three basic considerations: ecological viability, social desirability, and economic feasibility. This is the challenge for current and future research endeavors.

LITERATURE CITED

Aguirre de L., R., J. Gasto C. and R. Nava C. 1976. Estructuras de escurrimiento y captacion en pastizales resembrados en el norte de Zacatecas. Univ. Aut. Agraria Antonio Narro Monografia Tecnico-Cientifica 2: 101-144. Saltillo, Coahuila, Mexico.

CNIZA. 1975. Informe de actividades. El Centro Nacional de Investigaciones para el Desarrollo de Zonas Aridas. CNIZA. Boletin Tecnico No. 1. Univ. Aut. Agraria Antonio Narro. Soltillo, Coahuila, Mexico.

De La Cruz C., J. A. and M. Zapien B. 1974. El Campo Experimantal Forestal de Zonas Andas La Sauceda, Rano, Anizpe Coahuila. Lineas de Investigacion y Resultedas. INIF Bol. Div. No. 36, SAG. Mexico.

De La Cruz C., J. A., M. Zapien B., M. Estrella M., J. G. Noriega L., J. A. De La Cruz B., R. Vasquez A. 1972. Reporte del estudio de la vegetacion de los campos experimentales "Noria de Guadalupe", Zacatecas, Ocampo, Coahuila, Matehuala, S.L.P., y Cuencame, Dgo., del Antonio Narro. Saltillo, Coahuila, Mexico. Mimeo.

Fierro, L. C. 1974. El manejo de pastizales y la investigacion en Mexico. In: Dpto. de Recursos Naturales Renovables (Ed.). Memorias del Primer Congreso Nacional sobre Manejo de Pastizales. Univ. Aut. Agraria Antonio Narro., Saltillo, Coahuila, Mexico.

Flores A., E. 1980. Establecimiento de pastizales de secano en diferentes sistemas de cosecha de agua en el Norte de Mexico. Tesis Profesional, Ing. Agr. Zootecnista. Univ. Aut. Agraria Antonio Narro. Saltillo, Coahuila, Mexico.

Frias H., J. T. 1981. Dinamica de Atriplex canescens (Pursh) Nutt. establecida en estructuras de poceo mediante siembra directa en Ocampo, Coahuila. Tesis Profesional, Ing. Agr. Zoot., Univ. Aut. Agraria Antonio Narro. Saltillo, Coahuila, Mexico.

Galicia S., S. 1980. Efecto de diversas relaciones area:siembra:area escurrimiento en el establecimiento de pastizales. Tesis Profesional, Ing. Agr. Zoot., Univ. Aut. Agraria Antonio Narro. Saltillo, Coahuila, Mexico.

Garza C., H. M., J. G. Medina T. and G. Gloria H. 1985. La resiembra como estrategia de tranformacion del pestizales. In: De Luna V., R., J. G. Medina T. and L. C. Fieno (Ed.). Manejo y Transformacion de Pastizales. Secretario de Desarrollo Urbano y Ecologia. Saltillo, Coahuila, Mexico.

Garza C., H. M., J. G. Medina T., L. E. Rodriguez G. 1982. Water catchment systems to establish blue and sideoats grama in Mexico. Paper presented at the 35th Annual Meeting, Society for Range Management. Calgary, Canada.

Garza C., H. M., J. G. Medina T. and J. Gasto C. 1978. Soil surface modification and reseeding arid ranges in northern Mexico. Paper presented at the 31st Annual Meeting, Society for Range Management. San Antonio, Texas.

Garza C., H. M., J. G. Medina T., J. Gasto C. and R. Armijo T. 1977. Transformacion de ecositemas aridos de pastizal. Estrategias de establecimiento. Univ. Aut. Agraria Antonio Narro Monografia Tecnico-Cientifica 3: 63-181. Saltillo, Coahuila, Mexico.

Gloria H., G., J. G. Medina T., H. Garza C. and R. De Luna V. 1978. Evaluacion de estrategias para el mejoramiento de pastizales aridos. Univ. Aut. Agraria Antonio Narro, Monografia Tecnico-Cientifia 4: 234-284. Saltillo, Coahuila, Mexico.

Gonzalez, D., J. 1974. Influencia del tamano del area de escurrimeinto en el desarrollo comparativo de seis gramineas forrajeras. CNIZA, Boletin Tecnico No. 3 pp:13-18. Univ. Aut. Agraria Antonio Narro. Saltillo, Coahuila, Mexico.

Gonzales, M. H. and L. C. Fierro. 1985. Estado actual de los pastizales y posibles soluciones para la ganaderia del norte de Mexico. In: De Luna V., R., J. G. Medina T. and L. C. Fierro (Ed.). Manejo y Transformacion de Pastizales. Secretaria de Desarrollo Urbano y Ecologia. Saltillo, Coahuila, Mexico. 335 p.

Ibarra, F. A., H. M. Garza C. and R. De Luna V. 1980. Utilization of pitting structures for the establishment of four-wing saltbush (Atriplex canescens pursh) Nutt. in northern Mexico. Paper presented at the 33rd Annúal Meeting, Society for Range Management, San Diego, California.

Martinez M., L. and L. Maldonado. 1973. Zonas aridas. Recuros vegetales. Productora Nacional de Semillas. Bol. Div., Secretaria de Agricultura y Ganaderia. Mexico, D. F.

Medellin-Leal, F. 1982. The chihuahuan desert. In: Bender Gordon L. (Ed.). Reference handbook on the deserts of North America 6: 321-381 West Port, Greenwood Press.

Mellado B., M., J. G. Median T., J. A. De La Cruz C. and M. Zapien B. 1976. Transformacion sucesionalde la comunidad de Larrea Flourensia en el desierto Chihuahuense. Univ. Aut. Agraria Antonio Narro, Monografia Tecnico-Cientifica 2: 490-556. Saltillo, Coahuila, Mexico.

Medina T., J. G., F. Elizondo R. and R. De Luna V. 1986. Water harvesting systems for improving range seeding in Durango, Mexico. Paper presented at the 39th Annual Meeting, Society for Range Mangement, Kissismee, Florida.

Medina T., J. G., R. De Luna V. and L. C. Fierro. 1985. Desarrollo del manejo de pastizales. In: De Luna V., R., J. G. Medina T. and L. C. Fierro (Ed.) Manejo y Transformacion de pastizales. Secretaria de Desarrollo Urbano y Ecologia. Saltillo, Coahuila, Mexico.

Medina T., J. G. 1976. Harvesting surface runoff and ephemeral streamflow in arid zones. In: Kunkle, S. H. and J. L. Thames (Ed.). Conservation in arid and semi-arid zones. FAO Conservation Guide No. 3. Rome.

Munoz C., S. and M. Castro G. 1974a. Mejoramiento de agostaderos mediante microcuencas y siembra parcial de pastos. CNIZA, Boletin Technico No. 1. Univ. Aut. Agraria Antonio Narro. Saltillo, Coahuila, Mexico. 18 p.

Munoz C., S. and M. Castro G. 1974b. El trazo esmerado de curvas a nivel y su efecto en el costo, establecimiento y produccion de pastos en agostaderos. CNIZA, Boletin Technico No. 3: 1:19, Univ, Aut. Agraria Antonio Narro. Saltillo, Coahuila, Mexico.

Munoz C., S. and F. Elizondo R. 1974.
   Comparacion de practica para la siembra de
   zacate rhodes en agostaderos. CNIZA,
   Boletin Tecnico No. 3: 21-27. Univ. Aut.
   Agraria Antonio Norro. Saltillo,
   Coahuila, Mexico.

Nava C., R., R. Armijo and J. Gasto. 1977.
   Investigacion silvoagropewana de los zonas
   aridas Mexico. Campo experimental
   Noria de Guadelupe. Univ. Aut. Agraria
   Antonio Norro. Monografia
   Tecnico-Cientifica 3: 182-265. Saltillo,
   Coahuila, Mexico.

Reynaga V., R., J. G. Medina T., J. A. De La
   Cruz C. and M. Zapien B. 1976.
   Productividad de patizales resembrados en
   la region arida del sur de Coahuila.
   Univ. Aut. Agraria Antonio Narro,
   Monografia Tecnico Cientifica 2: 149-283.
   Saltillo, Coahuila, Mexico.

Rodriguez G., L. R. 1980. Alternativas
   arquitectocnicas de ecosistemas en las
   comunidades naturales de la zona arida del
   Norte de Mexico. Tesis Profesional, Ing.
   Agr. Zootechnista, Univ. Aut. Agraria
   Antonio Narro. Saltillo, Coahuila,
   Mexico.

Rodriguez R., E., R. Nava C. and J. Gasto C.
   1976. Comparacion de practicas de
   resiembra de pastizales de secano en el
   norte de Zacatecas. Univ. Aut. Agraria
   Antonio Narro Monografia
   Tecnico-Cientifica 2: 58-100. Saltillo,
   Coahuila, Mexico.

RANGE SEEDING EQUIPMENT

by Dan W. McKenzie[1]

ABSTRACT

This paper calls the reader's attention to some
of the more commonly used range seeding
equipment. For a more complete listing, the
annual reports of the Vegetative Rehabilitation &
Equipment Workshop and their publication,
Catalog; Revegetation Equipment should be
reviewed. Some of the listed equipment is
available commercially but most of the equipment
has to be assembled by the user.

INTRODUCTION

A prime source for information on range seeding
equipment and range rehabilitation equipment is
the publications of the Vegetative Rehabilitation
and Equipment Workshop (VREW). VREW is an
informal organization interested in developing
and testing revegetation equipment and providing
information about suitable equipment to land
managers. The organization consists of Federal
and State agencies plus private groups working to
improve rangelands and further range equipment
technology. The original name of VREW was
Reseeding Equipment Development Committee
(1946-1948). In 1949 the name was changed to
Range Reseeding Committee and in 1959 it was
shortened to Range Seeding Committee. In 1974
the name was again changed, this time to
Vegetative Rehabilitation and Equipment Workshop
or VREW. VREW may not have range or seeding in
its name now but it is still deeply involved with
range seeding and range seeding equipment.

VREW, including the most recent meeting in Boise,
Idaho, in February of this year, has met
forty-one times to review accomplishments, to
discuss development activities and to present new
information concerning revegetation equipment and
techniques. This organization, through its
annual report and other publications, has
sponsored development of, reviewed, or reported
on many types and designs of range seeding
equipment and related revegetation equipment. The
most widely used range seeding implement is the
Rangeland Drill which was developed under the
sponsorship of VREW. This implement along with
many other pieces of range seeding equipment is
described in the publication of VREW titled
Catalog; Revegetation Equipment, (Lawson, 1980)

---

1 Mechanical Engineer, USDA, Forest Service,
  Equipment Development Center, 444 East Bonita
  Avenue, San Dimas, California 91773 and former
  Information and Publication Workgroup chairman,
  Vegetative Rehabilitation and Equipment
  Workshop.

Equipment for range seeding can be classified
into two groups--ground preparation equipment and
seeding equipment. Sometimes the ground
preparation equipment serves as the seeding
equipment when equipped with seed distribution
hardware or seed boxes.

GROUND PREPARATION EQUIPMENT FOR RANGE SEEDING

Ground preparation equipment aids plant
establishment by conditioning the soil,
preventing erosion, and retaining moisture.
Ground preparation equipment may include but is
not limited to the following.

Anchor Chains

An anchor chain, pulled between two tractors, has
been a standard brush control and ground
preparation procedure for many years. Much of
the appeal of chaining lies in its high
production rate and low cost. Chaining is often
used in preparation for burning prior to
broadcast seeding. Broadcast seeding can also be
done before chaining for the action of the chains
usually provides sufficient soil disturbance to
cover the broadcasted seed. Three basic chains
are in use for ground preparation--smooth chain,
Ely chain, and the Dixie Sager.

Smooth Chains

Smooth or unmodified chains are not very
effective for ground preparation and are not
widely used. Young and flexible plants are not
effectively removed. For plant removal with
smooth chains individual links must weigh 90 lb
or more and the plants must be large and brittle.

Ely Chain

The Ely chain is a modified anchor chain with
steel railroad rails (approximately 18-in long)
welded across each chain link resulting in about
a 4-in projection out each side of the link at
right angles to the link. This modified chain,
when pulled between two tractors, results in
considerable ground disturbance.

Dixie Sager Chain

The Dixie Sager chain is also a modified anchor
chain with railroad rails welded to each link of
the chain but with the rails welded lengthwise to
the chain links. This modified chain, when
pulled between two tractors, also results in
considerable ground disturbance.

Pipe Harrow

The pipe harrow consists of spiked pipes that are trailed behind a spreader bar. The pipes are attached to the spreader bar with swivels at equal intervals to allow the pipes to rotate freely and clean themselves of trash. The pipe harrow will thin low brittle shrubs, scarify the soil surface, and cover broadcasted seed.


Pipe Harrow in Operation

Root Plows

The root plow is a V-shaped blade mounted between two shanks attached to the toolbar of a crawler tractor. Fins are attached to the top of the V-blade to cut rhizomes and lift severed roots to the surface. Root plowing is often used with broadcast seeding.

Tandem Disk Plow

Tandem or offset disk plows consist of two rows or gangs of disks operated at an angle to each other. The angle is adjustable for varying soil conditions. The disks may have notched or straight edges. Most offset disks have wheels that are raised or lowered hydraulically to regulate operation depth and for use in moving the disk. Offset disks cannot be operated in soils which have many large rocks; when a large rock is encountered the entire weight of the disk gang may be carried by one or two disks blades, which can result in breakage of disk blade.

Brushland Plow

The Brushland Plow is a development of VREW. It consists of seven pairs of disks mounted on spring-loaded arms. The arms are attached to a heavy duty frame supported by three wheels. When an obstruction such as a large rock is encountered, the spring loaded arms allow each pair of disks to independently ride over the obstruction thus eliminating the problem with the tandem disk when used in areas with large rocks.
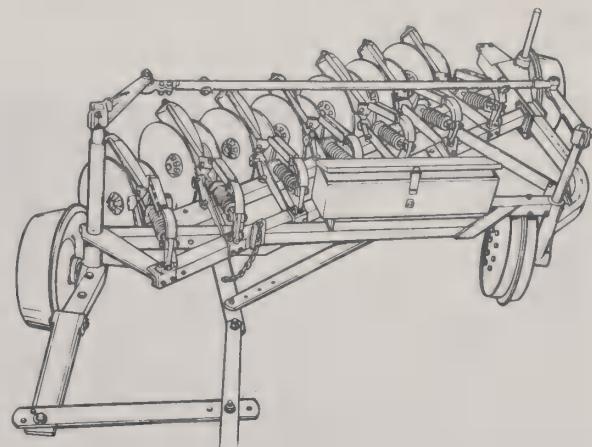
Brushland Plow

Contour Furrower

The Contour Furrower is another development of VREW. It is made up of four major components: two subsoilers, two pairs of offset disks, two four-blade paddlewheel dammers, and a seed box spreader. The Contour Furrower breaks up compacted soil, forms furrows, forms dams in the furrows, and broadcasts seed. It is used for reclaiming deteriorated rangelands, preventing soil erosion, and improving moisture conditions.

Contour Furrower

Disk Chain

The Disk Chain is a recent development sponsored
by VREW. The development work is being carried
out by the Texas Agricultural Experiment Station
of the Texas A & M University. The Disk Chain is
an anchor chain on which disks have been added,
this combines the best features of the anchor
chain and the disk. The anchor chain is a low
cost implement to operate as it can cover large
areas rapidly. The disk does a superior job of
seedbed preparation but is a much more expensive
method. The Disk Chain can cover large areas
rapidly, does a good job of seedbed preparation
and is low cost to operate.

Disk Chain

RANGE SEEDING EQUIPMENT

Range seeding equipment can take many forms. The
seed is either broadcast by various spreaders to
scatter the seed over the ground, or planted by
drills or planters to bury the seed at the
desired depth. Drilling the seed is the
preferred method because it uses the seed more
efficiently, places the seed more accurately, and
increases the probability of plant
establishment. Broadcast seeding general
requires 50 to 75 percent more seed in order to
obtain a comparable stand.

Rangeland Drill

The Rangeland Drill is a development of VREW.
This implement was designed for seeding
rangeland. It is rugged, versatile implement for
drilling on rough, rocky, and brushy areas. It
is the most widely used range seeding implement.
The Rangeland Drill is a very heavy-duty,
side-wheel drill. Its features include large
wheels which give it high clearance and
single-disk opener arms which are independently
suspended. The Drill can be equipped with deep
furrow arms with carry 24-in disks. Other
options available include: a small-seed hopper
attachment, a fertilizer attachment, a brush
guard to protect the running gear, and steel
wheels for use in areas with numerous brush snags
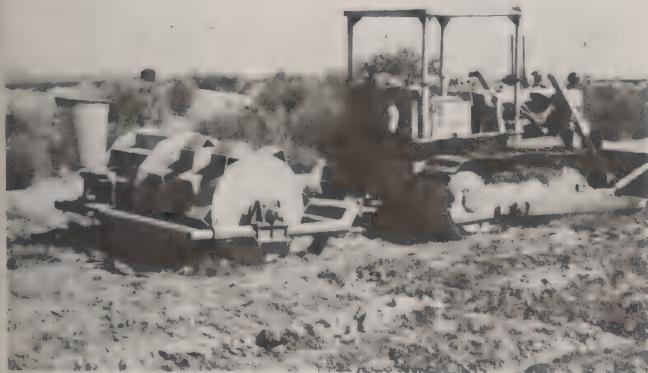where rubber tires cannot be used.
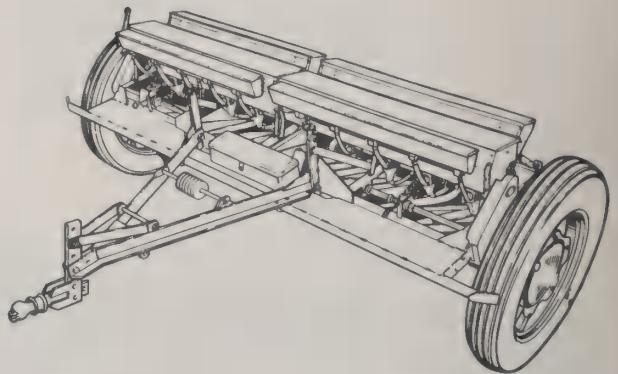
FRONT VIEW
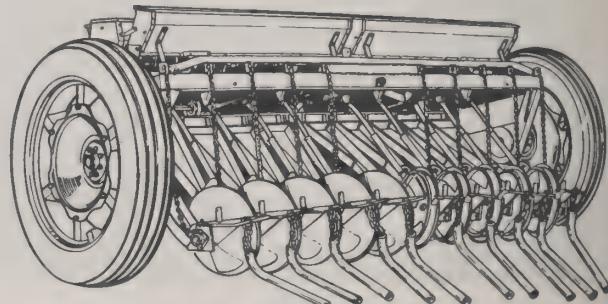
REAR VIEW

Rangeland Drill

Interseeder for Rocky and Brushy Areas

The interseeder for rocky and brushy areas was
designed specially for rough range land
conditions. It can create deep, wide furrows,
plant a wide variety of seeds, and operate
effectively on rocky and brushy ground. This
seeder consists of a small crawler tractor, an
implement carrying hitch, a ground working tool
or implement, a thimble seeder seed dribbler, a
pneumatic seed transfer system, and a chain
drag. Ground working tools or implements tried
or used have included fireplows, double disk
(Holt) trenchers and Rocky Mountain single-disk
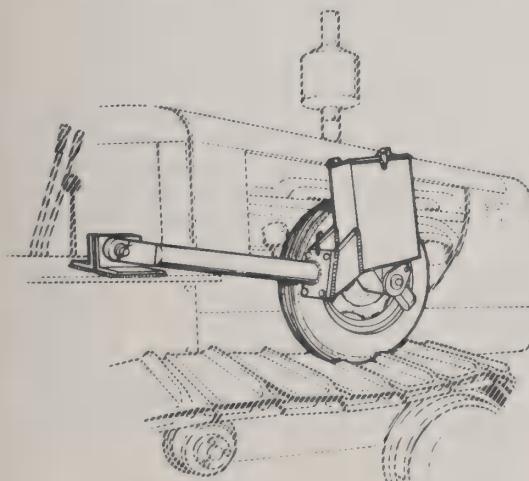trenchers. The fireplow is by far the most
effective.

262

Interseeder for Rocky and Brushy Areas

Seed Dribbler

Seed dribblers are small, traction wheel driven broadcast seeders that are mounted on a crawler tractor directly above a track. The traction wheel rests on and is driven by the track of the crawler tractor. Seed is dribbled directly onto the track. It is then carried forward and dropped on the ground in front of the advancing track where it is pressed into the ground. The compacted soil under the track provides a firm seedbed to hold moisture and enhance plant establishment and growth. Seed Dribbles can have fluted feeds or thimble seed metering mechanisms. The fluted feed is similar to the seed metering device found on most grain drills. The thimble metering device has small cups attached to spokes that rotate through the seed hopper. Both metering devices are adjustable to suit the kind of seed and desired seeding rate.

Seed Dribbler

Land Imprinter

The Land Imprinter is essentially a towed rolling chopper with two interchangeable drums mounted on a common axle. Several different drums are available to obtain a variety of imprinting patterns. The drums can be weighted by filling with water. A broadcast seeder and drag chains are mounted on the rear to spread and cover seed. The Land Imprinter creates a series of precise geometric patterns on the ground surface to control erosion and to direct rainwater infiltration. This is accomplished without tillage resulting in the soil structure and profile being preserved and the mulch material from the crushed brush being retained near the surface. The imprinting treatment produces an excellent, rainwater-irrigated seedbed for establishing grasses by broadcast seeding or rejuvenating native grass areas.

Land Imprinter

Hydraulic Seeder-Mulchers

Hydraulic seeder-mulchers consist of a tank, pump, and a discharge nozzle. The tank is equipped with agitators to assure uniform mixture. The hydraulic seeder-mulcher can apply seed, fertilizer, and soil amendments, including wood fiber mulch, in a water stream onto steep slopes without the necessity of operating a prime mover on the slope.

Grain Drills

Grain drills plant grain or grass on well prepared seedbeds. Granular or pelletized fertilizer is often applied along with the seed. Grain drills consist of furrow openers, seed metering devices, hoppers, and seed covering devices. The furrow openers may be chisel shanks, single disks, or double disks. Depth regulating bands are often attached to the disk openers to give precise depth control. Grain drills are suited for seeding smooth, well prepared seedbeds that are free from rocks and brush.

Pasture Drills

Pasture drills are heavy-duty grain drills
adapted for seeding grasses in stubble or
pastures without prior seedbed preparation.
Some pasture drills may also be used to seed
rangeland. Pasture drills are built on
heavy-duty frames to withstand the severe
requirements of grassland seeding. Most pasture
drills have double disk openers and large seed
tubes for precise placement of grass seed, but
some have flexing runners or chisel openers.
Some pasture drills are equipped with single-disk
coulters in front of the openers or have
heavy-duty press wheels behind the openers. Also
pasture drills often have hydraulic or
spring-loaded mechanisms to add additional down
pressure to the coulters or openers. The hoppers
are similar to the conventional grain drill and
may have baffles to insure uniform seed
distribution. Fertilizer hoppers are also
available on most pasture drills. Various
agitator and feed mechanisms have been adapted
for fluffy or chaffy grass seed. Pasture drills
may be towed or carried on a three-point hitch.

SUMMARY

This paper covers some of the most commonly used
range seeding equipment. For a more complete
listing of range seeding equipment refer to the
Catalog; Revegetation Equipment, (Lawson,
1908),publication of the VREW. Some range
seeding equipment is available commercially
(Rangeland Drill, grain drills, pasture drills
and Brushland Plow etc.) but most of the
equipment has to be assembled by the user. One
source of Rangeland Drills and Brushland Plows on
a loan basis is from the Bureau of Land
Management (BLM), Rangeland Rehabilitation
Equipment, Pool operated by the Vale District of
BLM, Vale, Oregon. This equipment when available
can be loaned to other Federal Government
agencies and also to farmers and ranchers through
agreements with the Soil Conservation service.

LITERATURE CITED

Larson, John E. 1980. Catalog: revegetation
    equipment. USDA Forest Service.
    Equipment Development Center, Fort Missoula,
    Montana 59801 198 pp

METHODS FOR ESTABLISHING GRASS SEEDLINGS

Victor L. Hauser[1]

ABSTRACT

Application of known physics of seeds and soil can improve the probability for success in grass establishment. Four methods that are based on physics may improve the probability for success in grass establishment, they are: punch planting, pregerminated seed, transplanting, and water applied in the seed furrow.

INTRODUCTION

Most range and pasture grasses must be established from seed because no practical field method is known for establishing them vegetatively. However, many grass seeds have low germination potential, are slow to germinate, and have poor seedling vigor. Grass seedlings are at a disadvantage because they must compete with vigorous, fast-growing weeds for soil water, nutrients, space, and sunlight.

A 3-year study of grass seeding in the Great Plains (Great Plains Council 1966) showed that seeding failures were common; more than 50% of seeding efforts produced failures in the humid areas of the Southern Great Plains. Seeding failures are common in all areas west of the Mississippi River in the United States. Failures reduce profits from grassland in at least 3 ways: 1) the cost of reseeding, 2) the loss of production from the land, and 3) failure to replace existing stands of poor quality forage with improved species because of the fear of seeding failure. Seeding failure may also increase soil erosion.

Most grass seeds should be planted less than 2 cm deep. However, the top 2 cm of soil may dry below the wilting point in one day or less, even in a subhumid climate or in winter in the Southwest (Army and Hudspeth 1960, Wiegand 1962, Reginato 1975). While soil water below the seed depth is often favorable for seedling growth, seeds may not germinate in the fast-drying seed zone, the roots may grow downward too slowly to stay ahead of the soil drying front or dry surface crusts may prevent emergence. Rapid drying of the seed zone soil is a major limiting factor for grass establishment from seed.

Many factors affect germination of seeds and establishment of seedlings; they are discussed by Wright (1971), Hillel (1972), Bewley and Black (1978), Black and Bewley (1982), McDonough (1977), and several authors in these Proceedings. This paper concentrates on the effects of water and temperature on germination and stand establishment and 4 methods that avoid rapid drying of seedbeds.

[1]Agricultural Engineer, USDA-ARS, Grassland, Soil and Water Research Laboratory, P.O. Box 6112, Temple, TX 76503-6112.

PHYSICS OF GERMINATION

After a healthy, living seed imbibes sufficient water, and if seed temperature is adequate, the complex chemical and biological process known as germination may begin. Numerous factors control the rate and degree of seed wetting, and thus control the germination process.

The soil water pressure difference between dry seed and moist soil is usually greater than 50,000 kPa (500 bars) (Hillel 1972). Thus, seed placed in wet soil hydrates rapidly at first. As seed water content increases, seed resistance to water flow is reduced (Young et al. 1983), but the pressure difference is also reduced. As water moves from soil to the seed, a thin layer of dry soil forms near the seed and soil resistance to water flow near the seed increases rapidly and may limit the rate of seed wetting. Rice grass seeds removed substantial amounts of water from soil up to a distance of 2.5 mm, but none from the soil beyond 10 mm from the seed (Bewley and Black 1978). The water content and physical properties of the soil within 2 or 3 mm of the seed controls seed wetting.

Soil water content is a major controlling factor for seed germination and seedling growth. Doneen and MacGillivray (1943) found that 18 vegetable crops germinated over the whole range of plant-available soil water, but 5 required soil water content near field capacity to germinate. They observed that seeds of all crops germinated in a shorter time at high soil moistures than at low. Hunter and Erickson (1952) found that germination occurred at soil water tensions between field capacity and -1270 kPa (-12.5 atm.) for corn, but the range for sugarbeets extended to only -350 kPa (-3.5 atm.). Gul and Allen (1976) showed that time to emergence for wheat doubled for each -400 kPa (-4 atm.) reduction of soil water potential. Hudspeth and Taylor (1961) found greatest emergence of Blackwell switchgrass (Panicum virgatum) at -34 kPa, field capacity.

Soil temperature is another major controlling factor for seed germination and seedling growth. Each species has its own optimum germination temperature, but good germination may occur over a wide range of temperatures. The adverse effects of water stress on germination and rate of seedling growth are increased for soil temperatures above or below the optimum (Hillel 1972, McGinnies 1960, Sharma 1976). Laude et al. (1952) found that soil temperatures above 52°C (125°F) prevented germination of six cool season grasses. Masiunas and Carpenter (1984a, 1984b) found no radicle growth at temperatures higher than 47°C (117°F) for 7 grasses and 5 legumes.

The degree of contact between the seed and water in the soil capillaries is a third major factor controlling germination of seeds. Sedgley (1963) and Manohar and Heydecker (1964) demonstrated that both rate and total seed germination were increased by larger area of contact between the seed and liquid water. Seeds with natural or artificial mucilage achieved better germination than seeds with no mucilage (Harper and Benton

1966). Soil particle size affects seed wetting and germination. Hadas and Russo (1974a) showed that soil particle size affects seed-to-soil contact area and that soil hydraulic conductivity interacts with particle size to control germination. Wet clay soil and wet sand produced the same rate of germination, but dry sand greatly reduced water flow rate to the seed and fewer seeds germinated in dry sand than in dry clay. Hadas and Russo (1974b) found that optimum seed-to-soil-water contact was achieved if soil aggregates were about one-fifth to one-tenth of the seed's diameter. Young et al. (1970) found that sub-clover germination was virtually zero at soil water pressures of -600, -800, and -1200 kPa (-6, -8, and -12 bars) on sand, loam, and clay soils, respectively. Bewley and Black (1978) stated that the area of contact between the seed and the soil is more important to germination than soil hydraulic conductivity.

As seeds hydrate they swell, thus increasing seed-to-soil contact area (Collis-George and Melville 1975). But, swelling may result in substantial mechanical pressure on seeds restrained by high-strength soils such as those prone to plow-pan formation. Collis-George and Williams (1968) showed that mechanical restraint delays seed germination even at low applied stress.

Seeds may imbibe water by absorbing water vapor from the soil atmosphere. The relative humidity of the soil atmosphere varies between 98 and 100% over the range of soil water contents which permit germination of most seeds (Hillel 1980). However, water vapor flow rate through soil is relatively low. Collis-George and Melville (1978) investigated the germination of wheat seeds by vapor flow only; 75% of seed separated from liquid water by 3 cm of saturated air germinated in 110 hours . However, wheat seeds separated from liquid water by 3 cm of 1.6-2.4 mm sand did not germinate. It is unlikely that commercially useful numbers of grass seeds can be germinated by water vapor flow through soils.

IMPROVED GRASS ESTABLISHMENT METHODS

Four grass establishment methods discussed below, avoid the adverse conditions created by rapid drying of the seedbed. The effects of temperature on germination and seedling growth are well known; accordingly, I assume that grass will be planted only during the season when soil temperatures are normally favorable for grass growth and that high quality seed will be used. The methods described below are attempts to use principles from the physics of seed germination to improve the probability for successful grass establishment.

Punch Planting

In the punch planting method, seeds are placed in the bottom of an open hole that is deeper than normal planting depth (fig. 1). The soil at the punch planting depth remains wet much longer than that at the conventional planting depth. Cary (1967) demonstrated that punch planting

established better stands of lettuce and carrots than conventional methods. Cary and Heinemann (1977), Heinemann et al. (1973), and Wilkins et al. (1979), invented and tested punch planting machines.
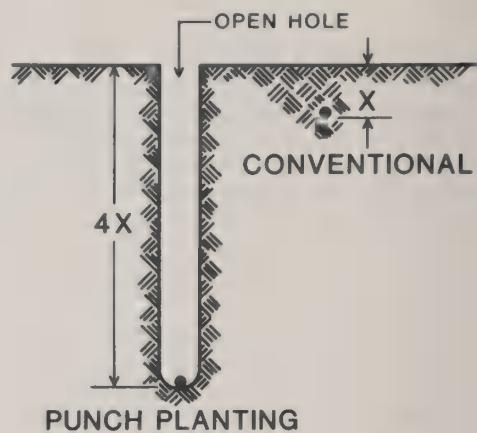

Figure 1. Punch planting vs. conventional planting.

Hauser (1982) tested punch planting for 5 range grasses: weeping lovegrass (Eragrostis curvula (Schrad.) Nees), kleingrass (Panicum coloratum L.), TAM wintergreen hardingrass (Phalaris aquatica), Kentucky 31 fescue (Festuca arundinacea), and eastern gamagrass (Tripsacum dactyloides (L.) L.). The tests were conducted in a greenhouse under dry conditions and in sandy loam soil. The drying rate of the greenhouse soil was typical of that found in the field in the Southern Plains (fig. 2). The soil at the conventional seeding depth dried to the wilting point in 3 days, but at the punch planting depth it was still wet at 10 days.
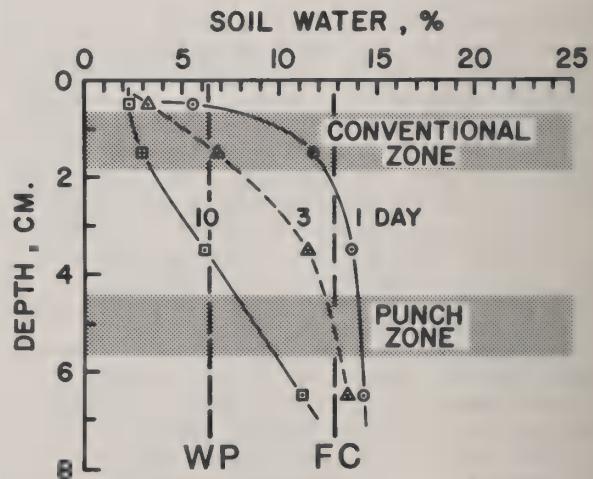

Figure 2. Typical soil water distribution (% by weight) in the surface layers in the greenhouse soil 1, 3, and 10 days after irrigation. The bands show the conventional or punch planting soil zones (0.5 cm water added after sampling on day 3).

Punch planting established significantly more plants than conventional planting methods when water was limited. The high soil-water content in the seed zone of punch-planted seeds improved germination of all species tested. The best hole diameter was the smallest that was tested, 0.6 cm. The best hole depth varied with species: 1.3-2.5 cm for lovegrass, 2.5-5 cm for kleingrass, and 5-10 cm for eastern gamagrass.

Two major problems limit the use of punch planting for range grasses; they are: 1) Rain may fill the holes with soil in field plantings thus burying the seeds too deep; and 2) The punch planting machines that are available are too slow and not rugged enough to work on rangeland. The concept of punch planting has much merit and might work well if these two problems were solved.

Pregerminated Seed

Pregerminated seeds grow fast enough to produce plants before the seedbed becomes too dry for germination and growth. The term pregermination is used in this paper and refers to seeds that were germinated to the point of radicle emergence before planting, never allowed to dry, and planted in a gel carrier. Gray (1981) states that pregerminated celery and carrot seeds were planted in small areas in the Netherlands, the United Kingdom, and the United States in the early part of this century.

In the experiments reported here, the seeds were germinated while suspended in a constant-temperature water bath with air injected through airstones in the bottom to aerate the water and keep the seeds in motion. When radicles were visible on about 5% of the seeds, they were removed from the water bath and suspended in gel. The gel was made from either Vitterra 2 Hydrogel Soil Amendment (Union Carbide Corp., Tuxedo, NY, Medical Products Division), or Laponite 508 (LaPorte (U.S.), Inc., Hackensack, NJ.).[2] They were planted in the greenhouse by placing both seed and gel into a conventional seed furrow. In the field, the suspension of seeds in gel was pumped through a roller pump and injected into a furrow opened by conventional double disk furrow openers.

The gels used to carry pregerminated seed are about 99% water. They are very slippery, so that soft, swollen seeds suspended in them move through simple roller pumps without damage. The gel acted as a seed carrier only since the water was absorbed into the soil within a few minutes or hours, depending on soil water content.

Hauser (1981) found that kleingrass seeds could be removed from the germinator and planted in the field just before most of the radicles emerged through the seed coat. Radicles were emerged from about 5% of the seeds. Therefore, it is not necessary to handle delicate seeds with long

radicles attached during planting. This simplifies the planting operation and the machines required to handle the seeds.

In greenhouse experiments, the pregermination treatment more than doubled the number of grass plants that were established under dry conditions (Hauser 1981). In field tests, the pregermination treatment produced up to twice as many grass plants as conventional seeding (Hauser 1983).

Hauser (1986b) evaluated 12 grass species to measure their response to pregermination. Four grasses produced significantly greater numbers of plants from pregerminated seeds than from untreated seeds; they were:

> Kleingrass (Panicum coloratum L.),
> Buffelgrass (Cenchrus ciliaris L), and
> Buffalograss (Buchloe dactyloides (Nutt.)
>   Engelm.).
> Weeping lovegrass (Eragrostis curvula
>   (Schrad.) Nees)

Switchgrass (Panicum virgatum L.) and blue panicum (Panicum antidotale Retz.) produced more plants from pregerminated seeds than from untreated seeds in one test, but not in the second test. Six grasses did not respond to pregermination treatment; they were:

> Sideoats grama (Bouteloua curtipendula
>   (Michx.) Torr.),
> Blue grama (Bouteloua gracilis (H.B.K.)
>   Lag. ex Steud),
> Big bluestem (Andropogon gerardii Vitman),
> Bahiagrass (Paspalum notatum Flugge),
> Green sprangletop (Leptochloa dubia (H.B.K.)
>   Nees), and
> Old world bluestem (Bothriochloa ischaemum).

Pregermination treatment produced at least an equal number of plants as compared to untreated seeds for all species tested.

Some, but not all, grasses produced much better stands of grass from pregerminated seeds than from untreated seeds, so we need to predict the response of individual species to pregermination. However, no pattern of response is evident from the studies cited above. Others investigated a similar problem; they soaked the seeds, then air-dried them before planting, they were not pregerminated (Chippendale 1934, Bleak and Keller 1970, 1972, 1974, Kastner et al. 1981, Lush and Groves 1981). Seed soaking improved establishment for some species, but not for others; no pattern of response is evident in their work either. Hence, it is necessary to test each grass species to prove that it will respond favorably to pregermination.

Kleingrass plants are drought tolerant; however, kleingrass seeds require a surprisingly high soil water content for best germination and plant establishment. Kleingrass produced best emergence when the soil water content was at or above field capacity between planting and first plant emergence (fig. 3) (Hauser 1986b). Kleingrass

---

[2]The use of trade names does not imply endorsement by the USDA.

produced markedly better plant emergence from pregerminated seeds than from untreated seeds under both favorable and unfavorable soil water regimes.
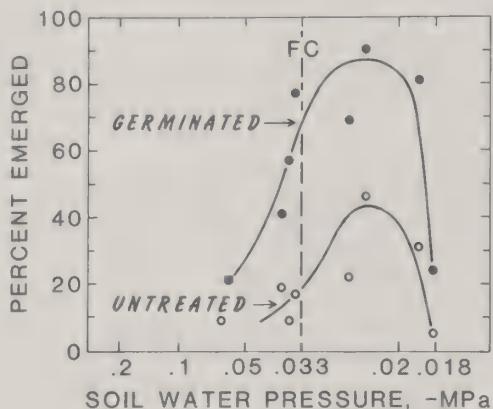

Figure 3. Percent of live untreated or pregerminated kleingrass seeds that produced plants 14 days after planting, as a function of the average soil water pressure of the 1- to 2-cm soil layer (seed zone). The independent variable is the average soil water pressure from day 0 to one day after first plant emergence, and the dashed line shows field capacity soil water pressure (Hauser, 1986b).

Transplanting

Transplanted seedlings avoid rapid drying of soil surfaces. A few grasses are established vegetatively now. For example, bermudagrass (Cynadon dactylon (L.) Pers.), is easily established by sprigging the stolons, rhizomes, and other plant parts into the field. Grass seedlings transplanted into the field survive and grow better than plants established from field seeding. Grasses are transplanted for research work; but, at present, transplanting is not used to establish grasses on a commercial scale, because of cost. Recent developments reduced the cost of transplanting, and there is now reason to believe that transplanting grass seedlings in the field will be both possible and economically feasible in the future.

There are two important requirements for success in transplanting grass: 1) mechanization to reduce labor cost and thus reduce transplanting cost and 2)high probability for success to reduce the cost of failure.

Brewer (1978) conceived the polyethylene bandoleer as a device in which to germinate seeds, grow seedlings, and automatically feed the seedlings into a transplanting machine in the field (fig. 4). The bandoleer is a container for seeds and seedlings and allows machine handling in all phases of production, including seeding, growing and transplanting into the field. The Agricultural Research Service developed a

transplanter around the intermittent dibble principle proposed by Moden et al. (1978). Equipment and machines to use the polyethylene bandoleer were developed and described by Moden and Hauser (1982), Hauser (1983), Ray and Hauser (1983), and Hauser (1985).
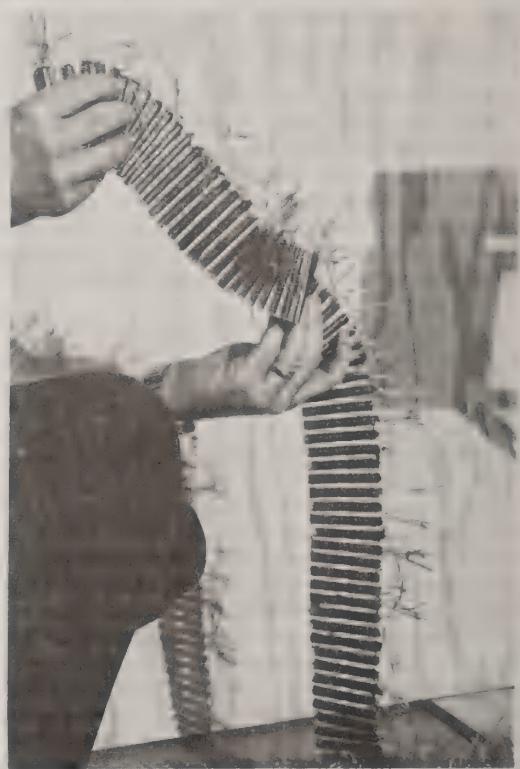

Figure 4. Polyethylene film, bandoleer belt holding kleingrass seedlings that are ready for transplanting.

The dibbling transplanter and the bandoleer fabrication methods developed at Temple, Texas, were moderately successful; the equipment is suitable for research, but not for commercial use. The machines proved that transplanting of grass is possible and demonstrated some of the requirements for success.

The plastic casing can be left on the root plug of grass seedlings, thus making machine handling and planting much easier (Moden and Hauser 1982, Hauser 1983). Two sizes of bandoleer cell (root plug) were tested, 0.8-cm diameter by 6-cm long (small), and 3.2-cm diameter by 11.4-cm long (large). Under adverse conditions such as drought or low temperature, the large cells were better than the small ones; however, the small bandoleers established good stands of grass under a wide range of conditions. Small cells reduce the cost per plant; thus the smallest practical size should be used.

The first transplanter employed an electronically controlled system to sense the presence of a transplant in position for planting (Moden and Hauser 1982). That system worked in the shop, but not in the field. Possible causes for machine malfunction included variation in optical density

of the plastic belt, foreign material in front of the photo cells, wind, machine motion, vibration, and deformation of the bandoleer belt by the foam rubber drive rollers (Moden and Hauser 1982, Hauser 1985). The electronically controlled mechanism had one strong point; it automatically rejected all bandoleer cells that contained no plant.

A mechanical feeding and shearing system successfully fed plants into the planting mechanism, but it planted all bandoleer cells, including those with no plant in them (Hauser 1985). Hauser (1985) also modified the rooting medium in the bandoleer cells to make them more rigid, thus improving machine performance.

Transplants set in the field by our transplanting machine suffered a very high death loss, but less than 20% of hand transplanted plants died. Additional work is required to find the cause of this problem. Possible causes of death include: 1) too much of the plant top was cut off just before planting, 2) adventitious root nodes formed too high on the plant, and 3) the plant root plug did not contain enough water to sustain the plant until new roots could grow into the soil.

Recent accomplishments by others have substantially advanced the science and art of growing and transplanting living plants into the field. Boa (1979, 1984) reported a successful system for automatically transplanting vegetables. Dedolf (1981) invented new transplanting machines. Masuda and Nambu (1979a, 1979b) invented transplanting systems that are in commercial use for transplanting about 74,000 ha of commercial sugarbeets annually in Japan (Kerr et al. 1986). A group working at the University of Nebraska developed procedures to use existing machinery for a largely automatic system for transplanting sugarbeets (Kerr et al. 1986, Smith et al. 1984, Yonts et al. 1984, Yonts et al. 1986). They report increased profits from sugarbeets of $60.00 per ha, and that 121 ha of sugarbeets were mechanically transplanted by commercial interests in Nebraska in 1985. In addition, numerous projects are underway to improve the automatic transplanting of trees.

These rapid improvements in transplanting technology offer hope that grasses can be successfully transplanted in the future.

Water in the Seed Furrow

The practice of applying a small amount of water in the open seed furrow is old. One vivid recollection from my childhood is that of carrying water in a bucket from the creek for my mother to pour on vegetable seeds in an open seed furrow. She then covered the wet soil and seed with dry soil. Both soil and climate were far from ideal at our garden site in western Oklahoma, but we obtained satisfactory stands of several vegetable species in the worst years.

Some seeds that are wetted by water immediately before planting germinate faster and at lower

soil water potential than seeds planted dry (Young et al. 1983, Collis-George and Hector 1966, Phillips and Youngman 1971). Doneen and MacGillivray (1943) state that germination of celery was improved by adding a drop of water to each seed after planting.

Three investigators applied water in the seed furrow to cultivated field crops. Fowler (1979) injected water into cotton seed furrows at planting and produced more plants and greater lint yield (26-41% increase) than from conventional planting. Noori et al. (1935) injected water into wheat seed furrows, and produced more wheat seedlings and greater yield (4-33% increase) than from conventional seeding. Wesley (1983) applied water in the seed furrow on soybeans planted in clay soil, and produced 4.7 times more seedlings than with no water.

Hauser (1986a) applied water in the seed furrow to 5 grass species in 10 experiments at two sites. The seeds were planted in a seed furrow opened by conventional double-disk furrow openers. Then water was added on top of the seeds and, finally the furrow was closed by conventional dual, angled press-wheels. Figure 5 shows typical results from that study.
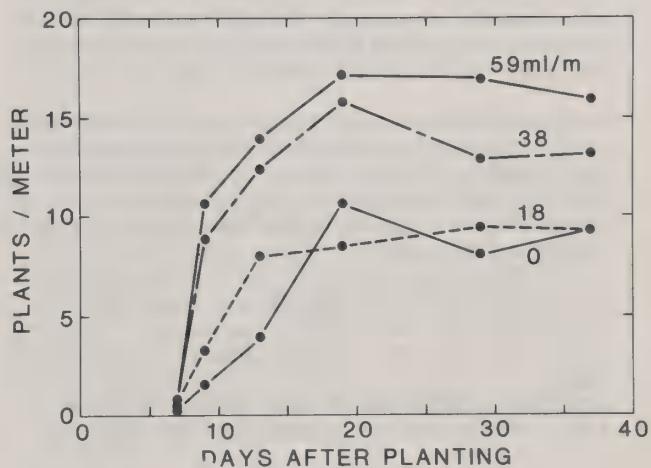

Figure 5. The number of living kleingrass plants/ meter established by 0, 18, 38, or 59 ml/m of water applied in the seed furrow. The seeding rate was 40 live seeds/meter (Hauser 1986a).

Water application was generally effective at rates of 38 ml/m of furrow or greater. Except under severe drought conditions, 60 ml of water/m of seed furrow doubled the number of plants established by seeds of 4 grass species. It doubled the number of plants established under both wet and dry conditions in clay soil. The water-in-the-furrow treatment was equal to or better than conventional seeding under extreme drought when the seeds lay in hot, sandy soil for 105 days. The application of water in the seed furrow may permit reduced seeding rates and improve the probability for success in grass establishment.

269

DISCUSSION

It is possible to improve the establishment of grasses from seed by using known principles of soil, water, and seed physics, even though much is still unknown about these subjects. Engineering can be effectively applied to develop improved systems for establishing grass plants.

The search for new and better methods for establishing range and pasture grasses is hindered by unwarranted emphasis on cost during research planning. Certainly, only cost-effective methods can be used in the field. The road to profit and efficiency on grasslands lies in the direction of more effective technology. It is not profitable to have vast areas of grassland covered by poor quality forage species. It is imperative that we learn how to effectively establish the desired grass species when and where they are needed.

CONCLUSIONS

All of the methods discussed utilize known physics of germination.

Punch planting is an excellent idea. There are two problems to overcome before it can be used effectively; they are: 1) stabilization of the punched hole, and 2) improved machinery to form the hole and place the seed.

The pregerminated seed concept can be profitably used now with existing machinery and readily available supplies. The main problem lies in the need to test each grass species individually to determine if pregermination will be effective with that species.

Transplanting technology is not ready for commercial use in establishing grass. However, the recent use of transplanting to establish sugarbeets on a field scale, and results of experiments with grass both suggest that we can find a way to use transplanting for grass.

It is easy to apply water in the seed furrow, and the practice is effective. Most ranchers and farmers own the needed equipment.

LITERATURE CITED

Army, T. J. and Elmer B. Hudspeth, Jr. 1960. Alteration of the microclimate of the seed zone. Agron. J. 52:17-22.

Bewley, J. D. and M. Black. 1978. Physiology and biochemistry of seeds in relation to germination. Vol. 1, Springer-Verlag, New York. 306 pp.

Black, M. and J. D. Bewley. 1982. Physiology and biochemistry of seeds in relation to germination. Vol. 2, Springer-Verlag, New York. 380 pp.

Bleak, A. T. and W. Keller. 1970. Field emergence and growth of crested wheatgrass from pretreated vs. nontreated seeds. Crop Sci. 10:85-87.

Bleak, A. T. and W. Keller. 1972. Germination and emergence of selected forage species following preplanting seed treatment. Crop Sci. 12:9-13.

Bleak, A. T. and W. Keller. 1974. Emergence and yield of six range grasses planted on four dates using natural and treated seed. J. Range Manage. 27:225-227.

Boa, W. 1979. Automatic transplanting. The Agric. Eng. 34:35-37.

Boa, W. 1984. The design and performance of an automatic transplanter for field vegetables. J. Agric. Eng. Res. 30:123-130.

Brewer, H. L. 1978. Automatic transplanter system for field crops. ASAE Paper No. 78-1011. ASAE, St. Joseph, MI. 19 pp.

Cary, J. W. 1967. Punch planting to establish lettuce and carrots under adverse conditions. Agron. J. 59:406-408.

Cary, John W. and William H. Heinemann. 1977. Magnetic seed delivery autodibble planter. U.S. Patent No. 4,061,094.

Chippendale, H. G. 1934. The effect of soaking in water on the "seeds" of some gramineae. Ann. Appl. Biol. 21:225-232.

Collis-George, N. and Jennifer B. Hector. 1966. Germination of seeds as influenced by matric potential and by area of contact between seed and soil water. Aust. J. Soil Res. 4:145-164.

Collis-George, N. and M. D. Melville. 1975. Water absorption by swelling seeds. I. Constant surface boundary condition. Aust. J. Soil Res. 13:141-158.

Collis, George, N. and M. D. Melville. 1978. Water absorption by swelling seeds. II. Surface condensation boundary condition. Aust. J. Soil Res. 16:291-310.

Collis-George N. and J. Williams. 1968. Comparison of the effects of soil matric potential and isotropic effective stress on the germination of Lactuca sativa. Aust. J. Soil Res. 6:179-194.

Dedolph, Richard R. 1981. Field transport systems and methods and components thereof. U.S. Patent No. 4,278,625.

Doneen, L. D. and John H. MacGillivray. 1943. Germination (emergence) of vegetable seed as affected by different soil moisture conditions. Plant Physiol. 18:524-529.

Fowler, J. L. 1979. In-furrow water injection for improving cotton stand establishment. Agron. J. 71:453-458.

Gray, D. 1981. Fluid drilling of vegetable seeds. Hort. Rev. 3:1-27.

Great Plains Council. 1966. A stand establishment survey of grass plantings in the Great Plains. Great Plains Council Rep. No. 23. 60 pp.

Gul, Azam and R. E. Allen. 1976. Stand establishment of wheat lines under different levels of water potential. Crop Sci. 16:611-615.

Hadas, A. and D. Russo. 1974a. Water uptake by seeds as affected by water stress, capillary conductivity, and seed-soil water contact. I. Experimental study. Agron. J. 66:643-647.

Hadas, A. and D. Russo. 1974b. Water uptake by seeds as affected by water stress, capillary conductivity, and seed-soil water contact. II. Analysis of experimental data. Agron. J. 66:647-652.

Harper, J. L. and R. A. Benton. 1966. The behavior of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. J. Ecol. 54:151-166.

Hauser, Victor L. 1981. Planting germinated grass seed. Trans. ASAE 24:1127-1130.

Hauser, Victor L. 1982. Punch planting to establish grass. J. Range Manage. 35:294-297.

Hauser, Victor 1. 1983. Grass establishment by bandoleers, transplants, and germinated seeds. Trans. ASAE 26:74-78, 80.

Hauser, Victor L. 1985. An automatic grass transplanting machine. Trans. ASAE 28:1777-1782.

Hauser, Victor L. 1986a. Water injection in grass seed rows. Trans. ASAE 29:1247-1253.

Hauser, Victor L. 1986b. Emergence of several grasses from pregerminated seed and some soil water effects. Agron. J. 78:206-210.

Heinemann, W. H., Jr., J. W. Cary, and A. E. Dilworth. 1973. Experimental machines for autodibble planting. Trans. ASAE 16:656-659.

Hillel, D. 1972. Soil moisture and seed germination. pp. 65-89. In Kozlowski, T. T. (ed.) Water Deficits and Plant Growth, Vol. III, Plant Responses and Control of Water Balance. Academic Press, New York. 368 pp.

Hillel, Daniel. 1980. Fundamentals of Soil Physics. Academic Press, New York. 413 pp.

Hudspeth, E. B. and H. M. Taylor. 1961. Factors affecting seedling emergence of Blackwell switchgrass. Agron. J. 55:331-335.

Hunter, J. R. and A. E. Erickson. 1952. Relation of seed germination to soil moisture tension. Agron. J. 44:107-109.

Kastner, W. W., Jr., C. J. Goebel, and J. C. MaGuire. 1981. Effects of a wet-dry seed treatment on the germination and root elongation of 'Whitmar' beardless wheatgrass under various water potentials. J. Range Manage. 34:305-307.

Kerr, Eric D., James G. Robb, John A. Smith, Robert G. Wilson, and C. Dean Yonts. 1986. Transplanting sugarbeets focus of IANR research. IANR Quarterly (Univ of Nebraska) 32:8-12.

Laude, Horton M., Jeffrey E. Shrum, Jr. and Wayne E. Bieler. 1952. The effect of high soil temperatures on the seedling emergence of perennial grasses. Agron. J. 44:110-112.

Lush, W. M. and R. H. Groves. 1981. Germination, emergence and surface establishment of wheat and ryegrass in response to natural and artificial hydration-dehydration cycles. Aust. J. Agric. Res. 32:731-739.

Manohar, Man Singh and W. Heydecker. 1964. Effects of water potential on germination of pea seeds. Nature 202:22-24.

Masiunas, J. B. and P. L. Carpenter. 1984a. Radicle growth of grasses and legumes in response to temperature. HortSci. 19:298-300.

Masiunas, J. B. and P. L. Carpenter. 1984b. Effects of temperature on radicle growth of Lolium multiflorum, Bouteloua curtipendula, and Lespedeza stipulacea. HortSci. 19:300-301.

Masuda, Akiyoshi and Tetsuo Nambu. 1979a. Continuous paper cylinder assembly and method of separating the same and transplanting apparatus for the same. U.S. Patent No. 4,132,337.

Masuda, Akiyoshi and Tetsuo Nambu. 1979b. Apparatus for separation and transplanting paper tube seedlings from a continuous paper tube seedling assembly. U.S. Patent No. 4,167,911.

McDonough, W. T. 1977. Seed physiology. pp. 155-187. In Sosebee, Ronald E. (ed.) Rangeland Plant Physiology. Range Sci. Series No. 4, Soc. Range Manage., Denver, CO. 290 pp.

McGinnies, William J. 1960. Effects of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-162.

Moden, W. L., Jr., T. W. Chappell, and F. H. Pitkin. 1978. An intermittent dibble-type container planter. Trans. ASAE 21:455-459.

Moden, Walter L., Jr. and Victor L. Hauser. 1982. An automatically-fed bandoleer transplanter. Trans. ASAE 25:864-867.

Noori, Fariborz, Floyd E. Bolton, and Dale N. Moss. 1985. Water injection at seeding of winter wheat. Agron. J. 77:906-908.

Phillips, J. C. and V. E. Youngman. 1971. Effect of initial seed moisture content on emergence and yield of grain sorghum. Crop. Sci. 11:354-357.

Ray, Kathryn A. and Victor L. Hauser. 1983. Making plastic bandoleers and growing plants in them. Grassland, Soil and Water Research Lab., P. O. Box 6112, Temple, TX 76503-6112. USDA, Agric. Res. Serv. AAT-S-30. 15 pp.

Reginato, R. J. 1975. Sampling soil-water distribution in the surface centimeter of a field soil. Soil Sci. 120(4):292-294.

Sedgley, R. H. 1963. The importance of liquid-seed contact during the germination of Medicago tribuloides Desr. Aust. J. Agric. Res. 14:646-653.

Sharma, M. L. 1976. Interaction of water potential and temperature effects on germination of three semi-arid plant species. Agron. J. 68:390-394.

Smith, John A., C. Dean Yonts, Robert G. Wilson, Eric D. Kerr, and James G. Robb. 1984. Paperpot system for mechanized sugarbeet transplanting. ASAE Paper No. 84-1516. ASAE, St. Joseph, MI. 10 pp.

Wesley, Richard A. 1983. Supplemental water for increased seedling emergence in soybean double cropping systems. ASAE Paper No. 83-1516. ASAE, St. Joseph, MI. 9 pp.

Wiegand, Craig L. 1962. Drying patterns of sandy clay loam in relation to optimal depths of seeding. Agron. J. 54:473-476.

Wilkins, D. E., P. A. Adrian, and W. J. Conley. 1979. Punch planting of vegetable seeds--A progress report. Trans. ASAE 22:746-749.

Wright, L. Neal. 1971. Drought influence on germination and seedling emergence. pp. 19-44. In Larson K. L. and Eastin, J. D. (eds.) Drought Injury and Resistance in Crops. Publ. No. 2, Crop Sci. Soc. Amer., Madison, WI.

Yonts, C. Dean, John A. Smith, Robert G. Wilson, James G. Robb, and Eric D. Kerr. 1984. Optimizing sugarbeet transplant spacing and container length. ASAE Paper No. 84-1517. ASAE, St. Joseph, MI. 8 pp.

Yonts, C. Dean, John A. Smith, Robert G. Wilson, Eric D. Kerr, and James G. Robb. 1986. Transplanted sugarbeet response to irrigation at transplanting. Trans. ASAE 29:1254-1258.

Young, James A., Raymond A. Evans, and Burgess L. Kay. 1970. Germination of cultivars of Trifolium subterraneum L. in relation to matric potential. Agron. J. 62:743-745.

Young, James A., Raymond A. Evans, Bruce Roundy, and Greg Cluff. 1983. Moisture stress and seed germination. Renewable Resource Center, Univ. of Nevada, 920 Valley Road, Reno, NV 89512. USDA, Agric. Res. Serv. ARM-W-36. 41 pp.

MANIPULATING GREENHOUSE CULTURAL CONDITIONS TO OPTIMIZE SURVIVAL OF GRASS TRANSPLANTS

Charles R. Tischler and Victor L. Hauser[1]

ABSTRACT

Using grass transplants could circumvent problems with establishment from seed. Transplants should be grown from high quality seed in plastic cells in a glasshouse with temperature and light control. Cultural conditions should be selected to control the depth of adventitious rooting.

INTRODUCTION

Transplanting grass seedlings into the field offers an alternative to direct seeding where stand establishment from conventional grass seeding is unpredictable (Hauser 1983). Prototype equipment was developed which successfully planted seedlings growing in plastic bandoleers (Hauser 1985, Brewer 1978, Ray and Hauser 1983). Transplanted seedlings have several advantages over conventional seeding. The seedling roots are several cm long at planting and they can grow downward immediately into moist soil and stay well ahead of the "drying front" as the soil progressively dries. Root growth can begin immediately after planting, whereas seeds sown in the field require two or more days of germination time before radicle elongation begins. Transplants may have a two to three week advantage in size and development over seed-derived seedlings; so they quickly grow big enough to survive damage by blowing sand, insects or rodents, and compete with vigorous weed species.

The chief drawback to transplanting grass seedlings is the cost of growing plants and transplanting them into the field. Labor is, at present, a major part of the high cost of transplanting. Automatic transplanting is economically feasable for high value horticultural crops. Grass seedlings should be transplanted if (a) direct seeding is unsuccessful, (b) the grass species planted can persist for many years, and (c) the new species will significantly improve the economic return from the land.

Although transplants can be grown and handled in many containers, we propose the plastic bandoleer system suggested by Brewer (1978). His plastic bandoleer has several advantages over other containers. It can be coiled in flats or folded in a serpentine mode into trays for efficient handling of large numbers of seedlings in one device. It can be moved and manipulated by machines and permits seeding, growing, and transplanting operations to be highly mechanized to reduce labor costs. In the following discussion, we assumed that plants will be

---

[1] Plant Physiologist and Agricultural Engineer, USDA-ARS, Grassland, Soil and Water Research Laboratory, P.O. Box 6112, Temple TX 76503-6112.

cultured in bandoleers, although the principles developed would apply equally well to other types of culture systems.

GERMINATION AND SEEDLING ESTABLISHMENT

Blank cells waste space in the glasshouse and they are a problem in the field. Perhaps a photocell and appropriate mechanism could be installed on the transplanter to skip blank cells (Moden and Hauser 1982). Optimum utilization of space requires that each bandoleer cell contain a seedling. Of course, the ideal situation would be to use a seedlot with 100% viability and rapid, synchronous germination, but few such seedlots are available. It is difficult to assess the possible negative effect of multiple plants per cell on subsequent survival in the field. Indirect evidence suggests that multiple plants per cell may reduce chances for establishment. In a study of native plant communities, Yeaton and Cody (1976) noted greater distances between larger plants. One could interpret this observation to indicate that when two plants are adjacent, size of each plant would be greatly reduced. In a study of microsite requirements for establishment of native grasses in the Edwards Plateau of central Texas, Fowler (1986) found that presence of litter and rocks, but not the proximity of another plant, increased rate of survival. From these two reports, we conclude that best establishment will require a single plant in each bandoleer cell.

Assuming that germination is relatively rapid and synchronous, we will consider the influence of less than optimum viability (compensated for by planting more than one seed per bandoleer cell) on subsequent numbers of blank cells and/or numbers of cells containing more than one plant. Table 1 presents probabilities of none, one, or several plants per cell given three seedlot germination percentages and varying planting rates per cell.

Table 1. Effect of seed quality and planting density on number of plants/cell.

No. of seed planted/ cell	Germ. (%)	Number of plants emerged/cell				
		0	1	2	3	4
1	90	10	90	----	----	----
2	90	1	18	81	----	----
3	90	.1	2.7	24.3	72.9	----
1	50	50	50	----	----	----
2	50	25	50	25	----	----
3	50	12.5	37.5	37.5	12.5	----
1	30	70	30	----	----	----
2	30	49	42	9	----	----
3	30	34.3	44.1	18.9	2.7	----
4	30	24.01	41.16	26.46	7.56	.81

The ideal situation would be to have a seedlot with 100% germination. Planting one seed per cell would produce one plant per cell. Perfect seedlots are seldom found, but one could expect a good quality seedlot to have 90% germination. An inspection of Table 1 demonstrates that one seed per cell is the optimum planting density. Planting two seed per cell decreases the number of "blanks" to 1%, but this is offset by the presence of duplicate plants in 81% of the cells. Planting three seed per cell is out of the question.

For many grass seedlots germination may be about 50%, thus creating a dilemma concerning planting density. One seed per cell results in 50% blanks, a very undesirable situation. Two seed per cell cuts the frequency of blanks to 25%, but results in duplicates in 25% of cells. Once again, three seed per cell results in far too many cells with multiple plants. Seedlots with germination potential of 30% probably are not appropriate for mechanical transplanting. In this situation, the number of cells having one seedling is maximized by planting three seed per cell. However, this planting density also yields 34% blanks and 21% of cells with two or more seedlings.

A possible alternative to the problem of blanks and duplicates would be to plant thickly and hand thin seedlings to one per cell. Hand thinning is not a promising option because we find that it damages remaining plants, disturbs the growing media, and is too expensive to use except for research.

The above discussion illustrates that grass species whose seedlots normally have low germination are poor candidates for mechanical transplanting. Data of Zemetra and Cuany (1984) indicate that Indian ricegrass (_Oryzopsis hymenoides_ (Roem. & Schult.) fits in this category. There are many other examples which could be cited. Also, if rapidity or uniformity of germination is a problem, "osmotic priming" or other seed pretreatments may offer possibilities (Heydecker and Gibbons 1978, Keller and Bleak 1969).

Perhaps the grower should produce his own seed. Commercial seedlots often contain immature seed, or were not stored properly. Seed age is an important consideration (Shaidaee et al. 1969). Because use of transplants will require orders of magnitude less seed per acre than normal seeding techniques, even daily hand-harvesting of seed of some species may be an appropriate use of resources. Hand harvesting would certainly insure greater seed size, and very likely greater seedling vigor.

An alternative to planting one or more seeds of unknown quality in each cell is to plant a single germinated seed in each cell. This can be accomplished with known techniques and available machines. First the seeds are germinated in a water bath until radicles emerge, then the germinated seeds are separated from the rest (Hauser 1981, Taylor et al. 1978). Finally, single germinated seeds are planted in each growing cell by machines similar to the FD 6300

seeding head made by Fluid Drilling Limited, available through Hackensack, Fluid Drilling Limited, Laporte USA, Hackensack, NJ.[2] These methods and machines are used in commercial production of vegetables.

Planting Depth in Bandoleers

Our field observations of transplants show that grass plants should form adventitious roots at or below ground level to insure seedling survival. Hyder et al. (1969) recognized two types of grass seedling morphology, "festucoid", where nodal adventitious roots arise from near planting depth, and "panicoid", where nodal adventitious roots arise from near the soil surface. In either case, the nodal adventitious roots arise from the coleoptilar node (or higher nodes). Given these respective morphologies, there are no advantages to planting panicoid grass seed more than a few mm below the surface of the culture media. However, for festucoid grasses, planting the seed two or more cm deep would situate the plant crown and nodal roots 2 cm below the top of the bandoleer. When the bandoleer is transplanted into the field (assuming the top of the bandoleer is placed at or slightly below the soil surface), seedlings derived from the 2 cm seed placement would have crowns set deeply enough in the soil to avoid rapid desiccation, which often occurs at the soil surface. Crowns set 2 cm deep in the soil are buffered from the wide diurnal temperature fluctuations experienced at the soil surface. Festucoid grasses should be seeded at a substantial depth in the bandoleer.

TEMPERATURE AND LIGHT CONTROL

Temperature Effects on Germination

As has been developed thus far, cultural conditions should be chosen to maximize rate of development of the grass seedlings. For maximum efficiency, several "batches" of seedlings should be produced per unit glasshouse area per season. We believe that a glasshouse facility would be required if seedlings suitable for transplanting were to be produced with any degree of predictability. Implicit in our concept of such a facility is some capability for temperature control. Our concerns for temperature control relate not so much to high temperature extremes (which can be avoided by use of ventilation or evaporative cooling systems), but rather to temperatures below optimum. Temperatures above ambient improve rate and/or extent of germination (Knipe 1973, Stubbendieck and McCulley 1976, Ellern and Tadmore 1967). A germinator with good temperature control could be used, with seedlings subsequently being moved to the glasshouse following germination. Such an approach would work for festucoid grasses, but would be unacceptable for panicoid grasses (for reasons to

---

[2] The use of trade names and citations of suppliers does not imply an endorsement by the USDA.

be given later). Thus, at least in the case of panicoid grasses, the glasshouse should possess adequate temperature control to allow maximum rates of germination and early seedling growth.

Speed of germination is important to transplant production. Published values of germination percentages often cover long periods of time (up to six weeks). For growing transplants, an index such as the "promptness index" (Scott et al. 1984), which also assesses rate of germination, is of greater value than total germination. Obviously, even if a species germinates in excess of 90%, it would not be adaptable to mechanical transplanting if this germination is achieved over a period of weeks.

Temperature Effects on Seedling Survival and Growth

Temperature can effect both seedling survial and growth. Stubbendieck and McCulley (1976) indicated that under controlled conditions, sand bluestem (Andropogon hollii Hack.) survival was greatest at 30C, and significantly lower at 25 or 35C. For photosynthesis and seedling growth, C_4 grasses have a higher temperature optimum than C_3 grasses (Jones 1985). Also, in general, cooler night temperatures reduce dark respiration and result in faster seedling growth. Ivory and Whitman (1978) present data demonstrating effects of different day/night temperature combinations on the growth of five C_4 grasses. Optimum growing temperature recommendations should be gleaned from the literature or measured for each species to be transplanted.

Light Effects on Plant Morphology

In panicoid grasses, the subcoleoptile internode elongates thus forcing the coleoptile tip to emerge through the soil surface (Hyder et al. 1969). Elongation of the subcoleoptile internode ceases when light strikes the tip of the coleoptile. Because nodal adventitious roots form at the coleoptilar node, which is essentially at the base of the coleoptile, it is very important that the coleoptilar node be at or below the soil surface. Continuous light should be supplied to the germinating seedlings until all seedlings have emerged to insure that subcoleoptile internode elongation ceases soon enough to prevent the coleoptilar node from being above the surface of the media. In addition, the intensity of light should be saturating for the system. Vanderhoeff et al. (1979), present data for corn (Zea mays L.) indicating the saturating light intensities required to stop subcoleoptile internode elongation. The light levels required are far in excess of what could be supplied in a commercal germinator. (This is why the use of a germinator was discounted earlier in the discussion). As no analagous data for forage grasses exist, the values of Vanderhoeff et al. are the best available.

For festucoid grasses, the coleoptile is the organ of elongation, and nodal adventitious roots arise at planting depth, as previously described. For these grasses, intense illumination during the emergence stage is not necessary.

Light Effects on Seedling Growth

Ideally, seedlings should be cultured in the presence of irradiance which is saturating for photosynthesis. As this is not practical in a glasshouse during early spring, at least some supplemental light should be available. Also, the effects of duration of light should be considered. In this context, Stubbendieck and McCulley (1976) demonstrated that sand bluestem seedlings perform best with a 12 hr photoperiod. If supplemental lighting is supplied, the glasshouse manager should very carefully select the source to be used. Although fluorescent-incandescent systems are economical, in general much more desirable plant growth is observed when metal halide lamps are employed (Duke et al. 1975, and references cited therein). Unfortunately, possible secondary effects of light source on plant development have not been well studied. Guerra et al. (1985) compared growth and yield of wheat (Triticum aestivum L.) grown under metal halide, high pressure sodium, and low pressure sodium lighting, and found that although grain yield did not differ between treatments, the plants grown under low pressure sodium lighting lodged at maturity. Subsequent investigation demonstrated that phenylalanine ammonia-lyase and tyrosine ammonia-lyase activities were lower in plants grown under low pressure sodium lighting. As these enzymes control flow of metabolites ultimately used in synthesis of lignin and tannins, a lower level of activity of the enzymes could well result in lower pest resistance and a "unhardened" type of growth habit. The specific wavelengths missing in the low-pressure sodium spectrum which were responsible for the alteration in enzyme activities have not been identified. Before a final decision about the type of lighting is made, the glasshouse manager should give careful thought to the type of seedlings to be grown (panicoid, festucoid, or both), as well as the prospects for receiving limited solar radiation during the time of year the glasshouse facility is to be used.

Clipping Effects on Seedling Growth

The current transplanter design (Hauser 1985) imposes limitations on the size of the seedling that can be transplanted. Thus, given the present equipment, grass seedlings must be clipped to within 2.5 cm from the top of the bandoleer cell. This clipping is probably both advantageous and disadvantageous, as photosynthetic area is lost, but transpirational area is also removed. For the most part, clipping studies deal with effects on mature grass stands, and not with effects on small seedlings. However, Bernardon et al. (1967) studied defoliation effects on cane bluestem (Andropogon barbinodis Lag.) at various stages of growth. Removal of 30, 60, or 90% of aboveground biomass at the pretiller (seedling)

stage had little effect on shoot or root weight compared to unclipped controls. This would suggest that, at least in the species concerned, one rather drastic clipping should not adversely affect survival. In 36-day-old Kentucky bluegrass (Poa pratensis L.) seedlings, clipping top growth to 2.5 cm slowed root growth for five days (relative to controls), and then the differences disappeared (Dunn and Engel 1971).

The lack of adverse effects of clipping in these two reports suggest that clipping to 2.5 cm should not adversely effect field survival of transplants. If experimentation demonstrated that clipping to this level did reduce survival, the transplanting equipment should be modified to allow handling of transplants with greater shoot lengths.

Controlling Disease, Maintaining Fertility

A good routine practice for culturing grass transplants would be the inclusion of a fungicide treatment. Falloon (1980) indicates that for a number of Lolium species in both glasshouse and field studies, fungicides greatly increased the number of emerging seedlings. Ehrenreich (1958) and Hull et al. (1971) reported similar results for four grasses used for range reseeding in the Great Plains.

In our experience, a weekly watering with full strength Hoaglands solution supplied adequate mineral nutrition. In a similar vein, Ayeke and McKell (1969) observed that supplying high levels of nitrate or phosphate did not improve growth in either a high or a low vigor grass.

SUMMARY

We have attempted to briefly outline some of the factors to be considered in producing grass seedlings for mechanical transplanting. The references cited should give at least a superficial coverage of many of the topics of concern. No mention was made about optimum age of seedlings at the time of transplanting. This age will vary with species, and also with the level of environmental control that is available in the glasshouse. Obviously, it must be determined experimentally. Our experience is that close cooperation between the Plant Physiologist and Agricultural Engineer is desirable, so that the seedling is compatable with the equipment that is to plant it. Also, ecological and climatic factors need to be considered when selecting an optimum time frame in which to transplant the grass seedlings. Finally, the inputs of an economist would be most desirable, so that the feasability of the operation could be assessed and alternative strategies could be considered.

LITERATURE CITED

Ayeke, Cyril Alende and Cyrus M. McKell. 1969. Early seedling growth of Italian ryegrass and smilo as affected by nutrition. J. Range Manage. 22, 29-32.

Brewer, H. L. 1978. Automatic transplanter system for field crops. ASAE Paper No. 78-1011, ASAE, St. Joseph, MI 49085.

Bernardon, Able E., Donald L. Huss, and Wayne G. McCully. 1967. Effects of herbage removal on seedling development in cane bluestem. J. Range Manage. 20:69-72.

Duke, William B., Roger D. Hagin, Julian F. Hunt, and Dean L. Linscott. 1975. Metal halide lamps for supplemental lighting in greenhouses: Crop response and spectral distribution. Agron. J. 67:49-53.

Dunn, J. H. and R. E. Engel. 1971. Effect of defoliation and root-pruning on early root growth from Merion Kentucky Bluegrass sods and seedlings. Agron. J. 63:659-663.

Ehrenreich, John H. 1958. Effects of certain fungicides on seed germination and seedling establishment of range forage plants. J. Range Manage. 11:22-27.

Ellern, Sigmund J. and Naphtali H. Tadmor. 1967. Germination of range plant seeds at alternating temperatures. J. Range Manage. 20:72-77.

Falloon, R. E. 1980. Seedling emergence responses in ryegrass (Lolium spp.) to fungicide seed treatments. New Zealand J. Agric. Res. 23:385-391.

Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. Amer. Midl. Nat. 115:131-145.

Guerra, Daniel, Anne J. Anderson and Frank B. Salisbury. 1985. Reduced phenylalanine ammonia-lyase and tyrosine ammonia-lyase activities and lignin synthesis in wheat grown under low pressure sodium lamps. Plant Physiol. 78:126-130.

Hauser, Victor L. 1981. Planting germinated grass seed. Trans. ASAE 24:1127-1130.

Hauser, Victor L. 1983. Grass establishment by bandoleers, transplants, and germinated seeds. Trans. ASAE 26:74-78,80.

Hauser, Victor L. 1985. An automatic grass transplanting machine. Trans. ASAE 28:1777-1782.

Heydecker, W. and B. M. Gibbons. 1978. Attempts to synchronise seed germination. Acta Hortic. 72:79-92.

Hull, A. C., Jr and K. W. Kreitlow. 1971. Grass seedling emergence and survival after treatment with fungicides. J. Range Manage. 24:383-385.

Hyder, D. N., A. C. Everson, and R. E. Bement. 1969. Seedling morphology and seeding failures with blue grama. J. Range Manage. 24:287-292.

Ivory, D. A. and P. C. Whiteman. 1978. Effect of temperature on growth of five subtropical grasses. I. Effect of day and night temperatures on growth and morphological development. Aust. J. Plant Physiol. 5:131-148.

Jones, C. Allan. 1985. C4 Grasses and Cereals Growth, Development, and Stress Response. John Wiley & Sons, New York. 419 pp.

Keller, Wesley and Alvin T. Bleak. 1969. Root and shoot growth following preplanting treatment of grass seed. J. Range Manage. 22:43-46.

Knipe, O. D. 1973. Western wheatgrass germination as related to temperature, light, and moisture stress. J. Range Manage. 26:68-69.

Moden, Walter L., Jr. and Victor L Hauser. 1982. An automatically-fed bandoleer transplanter. Trans. ASAE 25:864-867.

Ray, Kathryn A. and Victor L. Hauser. 1983. Making plastic bandoleers and growing plants in them. USDA, Agric. Res. Serv., AAT-S-30. 15 pp. (Available from USDA-ARS, P. O. Box 6112, Temple, TX 76503-6112.)

Scott, S. J., R. A. Jones, and W. A. Williams. 1984. Review of data analysis methods for seed germination. Crop Sci. 24:1192-1199.

Shaidaee, Goodarz, Billie E. Dahl, and Richard M. Hansen. 1969. Germination and emergence of different age seeds of six grasses. J. Range Manage. 22:240-243.

Stubbendieck, J. and Wayne G. McCulley. 1976. Effect of temperature and photoperiod on germination and survival of sand bluestem. J. Range Manage. 29:206-208.

Taylor, A. G., J. E. Motes, and H. C. Price. 1978. Separating germinated from ungerminated seed by specific gravity. Hort. Sci. 13:481-482.

Vanderhoef, Larry N., Peter H. Quail, and Winslow R. Briggs. 1979. Red light-inhibited mesocotyl elongation in maize seedlings. II. Kinetic and spectral studies. Plant Physiol. 63:1062-1067.

Yeaton, R. I and M. L. Cody. 1976. Competition and spacing in plant communities: The northern Mohave desert. J. Ecol. 64:689-696.

Zemetra, Robert S. and Robin L. Cuany. 1984. Variation for lemma thickness in Indian ricegrass: Implications for dormancy, scarification, and breeding. Crop Sci. 24:1082-1084.

CONCEPTS AND PRINCIPLES OF THE WOODWARD CHAFFY
SEED CONDITIONING SYSTEM

C.L. Dewald[1], Aaron Beisel[2], and P.L. Sims[3]

ABSTRACT

The 'Woodward Chaffy Seed Conditioning System'
combines new concepts in mechanical conditioning
with new uses of aerodynamic principles into a
system which greatly improves the quality of
chaffy seeds. The system has been substantially
improved since its introduction in 1983 through
the use of pneumatic drives and new approaches
to air amplification and seed quality classifi-
cation.

INTRODUCTION

Unprocessed chaffy seed is usually a hetero-
geneous mix of stems, leaves, chaff, awns, hairs,
empty glumes and seed of various size and quality.
Natural dispersal agents such as hairs and awns
tend to cling to each other causing the seed
material to adhere in a mass and form "bridges"
making uniform dispensing and placement difficult.
Gravitational separation of the seed by differen-
tial mass and densities occur in the seed
storage and transport and, especially, in the
drill box and often result in non-uniform
seeding rates and stand failures. The 'Woodward
Chaffy Seed Conditioning System' (Dewald, et al.,
1983) combines uniform seed dispersing, and
unique scalping concepts with air entrainment,
conveyance, fluidic acceleration and momentum
discrimination principles to improve the quality
of chaffy seed.

MECHANICAL CONDITIONING

Mechanical components are designed to break-up
and loosen the entangled seed material for
uniform dispensing and to remove stems, leaves
and light debris prior to air entrainment
(Beisel, 1985a).

Uniform Seed Delivery

Uniform delivery of chaffy seed has been a
primary problem in most conditioning systems.
Conveyor belts and paddles deliver the seed
material in clumps which ball-up and clog

[1]Research Agronomist, USDA, ARS, Southern Plains
 Range Research Station, 2000 18th Street,
 Woodward, OK 73801
[2]Aaron's Engineering, Fargo, OK 73840
[3]Range Scientist, USDA, ARS, Southern Plains Range
 Research Station, 2000 18th Street, Woodward,
 OK 73801

conditioning systems. Roll type feeders have not
worked well due to bridging-over and non-uniform
dispensing of chaffy seed. The Woodward system
utilizes a variable-speed, tumbling basket
dispenser (fig. 1) to achieve uniform distribution.
Seed material within the basket is subjected to a
tumbling action which loosens and breaks up the
entangled chaffy seed allowing individual particles
to fall through openings in the cylindrical
tumbler at a rate controlled by the speed of
tumbling and the size of the openings. The rota-
tion speed of the tumbling basket was formerly
controlled by a five speed transmission powered
by a .37 kW electric motor (fig 1). Substitution
of an air driven (pneumatic) motor resulted in a
much wider range of tumbling speeds (5 to 200 rpm)
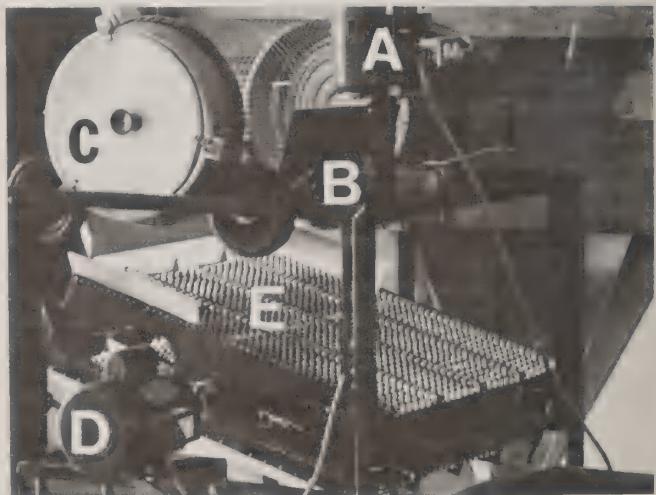compared to the former electric motor drive.

Figure 1. Mechanical conditioning components of
the 'Woodward Chaffy Seed Conditioning
System'. (A) Electric motor and (B)
five speed transmission formerly used
to drive the (C) tumbling feed basket.
(D) Electric motor formerly used as a
direct drive for the scalper decks.
(E) Slanted corrugated blade sieve for
removal of inert material.

Scalping

The removal of stems, leaves and light debris
(scalping) is necessary prior to air entrainment of
seed material to prevent plugging of the aerodynamic
components. Scalpers with flat surface screens
which utilize a back and forth motion and, or with
low intensity movement are not capable of efficient
trash removal from chaffy seeds. Removal of inert
material with the Woodward system combines the con-
cepts of slanted corrugated blade sieves an
oscillating (circular) motion and variable-speed
high intensity movement.

Sieve Construction

The scalping surface (sieve) is constructed of individual slanted blades made from 16 mm wide strips of .82 mm guage high chrome alloy stainless steel stamped in a corrugated pattern consisting of alternating ridges and grooves (fig. 2). The corrugated blades are secured to the scalper deck frame with the leading edge of each blade 12.8 mm distance from the leading edge of the adjacent blade. The blades are sloped to the rear at a 40° angle to the scalper deck frame so that when the scalper deck is placed at a 20° slope from horizontal, the slope of the blades are at a 20° angle to horizontal. This back slope allows the heavier seed material to fall through the scalper deck, whereas stems, leaves and lighter trash ride down the grooves and exit from the lower end of the scalper deck.

Slanted Corrugated Blade Sieve
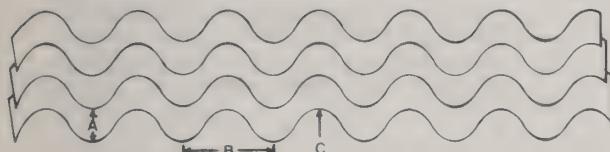
A = 12.8 mm from leading edge of blade to leading edge of the adjacent blade.
B = Corrugations are on 25 mm centers
C = Corrugation radius = 4.8 mm

Figure 2. The scalping surface (sieve) is constructed of individual corrugated blades which are secured to the scalper deck frame to allow seed to fall through and trash to ride over.

Oscillating Motion

The scalper deck oscillates at an amplitude of 1.5 to 2.3 mm in a circular motion causing seed to separate from each other and react as individual units rather than as a clinging mass which occurs when a strict back and forth motion is utilized.

Variable-Speed, High Intensity Movement

Chaffy seed are relatively light in mass and require a higher intensity of movement for separation than heavier materials. Previous models derived their intensity from an off-center weight powered by direct drive from a .37 kW electric motor to result in 1725 radians per minute (r/min.). The present models are powered by a single, air-driven, rotary-ball vibrator attached to the center of the scalper deck. Rotation speed can be varied from 1500 to 3000

r/min. as needed for different lots and kinds of chaffy seed for maximum scalping efficiency. The pneumatic, rotary-ball vibrator has resulted in 50 to 100% increase in scalping output and eliminated the necessity of the second (lower) scalping deck.

AERODYNAMIC CONDITIONING

Aerodynamic conditioning involves air entrainment, conveyence, fluidic acceleration, air-seed separation, and seed quality classification.

Power Heads

Power heads drive the aerodynamic system through pneumatic acceleration. They are used to create a positive air flow at the outlet and a negative air flow (vacuum) at the inlet. Seed material is air entrained as both seed and air flow into the inlet and are conveyed on to the power head where they are accelerated and discharged. Compressed air entering the power heads drives the aerodynamic components.

Ring-Jet Amplifier

The ring-jet amplifier (RJA) (fig. 3, fig. 4) is a new addition to our system. The RJA type power head produces a more laminar air flow with less turbulance and noise than the venturi type power head. The laminar air flow of the RJA power unit has resulted in superior seed quality classification without debearding or dehulling the seed.
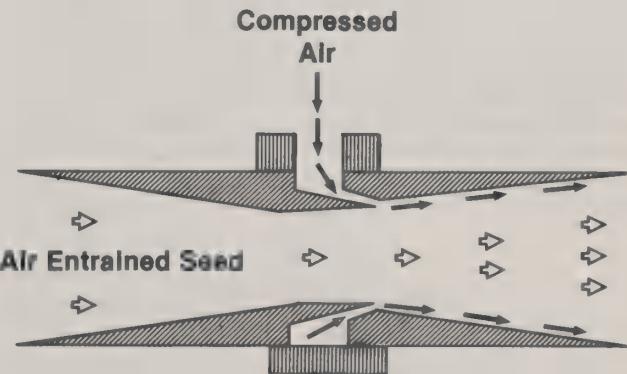
RING JET AIR FLOW AMPLIFIER

Figure 3. Diagramatic longitudinal view illustrating the action of the ring-jet amplifier power head.
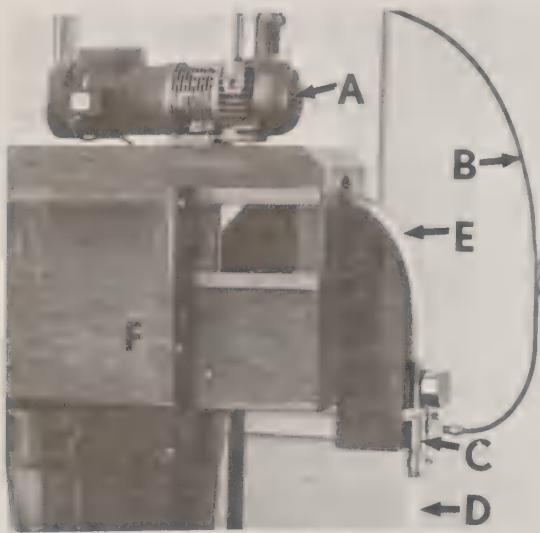
Figure 4. Aerodynamic conditioning components of the 'Woodward Chaffy Seed Conditioning System'. (A) Air compressor feeds compressed air through (B) air line to (C) ring-jet amplifier type power head. Air entrained seed enter the power head through the (D) inlet side and are accelerated through the (E) curved tube which separates the air from the seed by the skewed 'Coanda' Jet principle as it enters the (F) momentum discrimination chamber.

Venturi Accelerator

The venturi accelerator power head (fig. 5, fig. 6) is useful for debearding or dehulling chaffy seed. It produces a turbulant air blast which impacts and accelerates the seed to high speeds which strips off unwanted appendages. The size relationship of the venturi nozzle to the venturi barrel and the amount of air pressure applied determines the degree of chaff removal. A . nozzle-barrel venturi ratio of 1:5 (3.2 to 16 mm) operated at 300-400 kPa will debeard seed whereas a ratio of 1:3 (3.2 to 9.6 mm) at 650-750 kPa will result in complete seed dehulling.
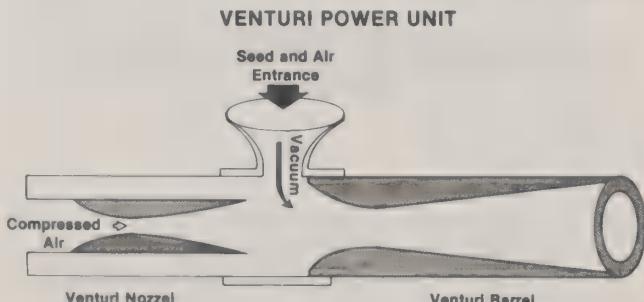

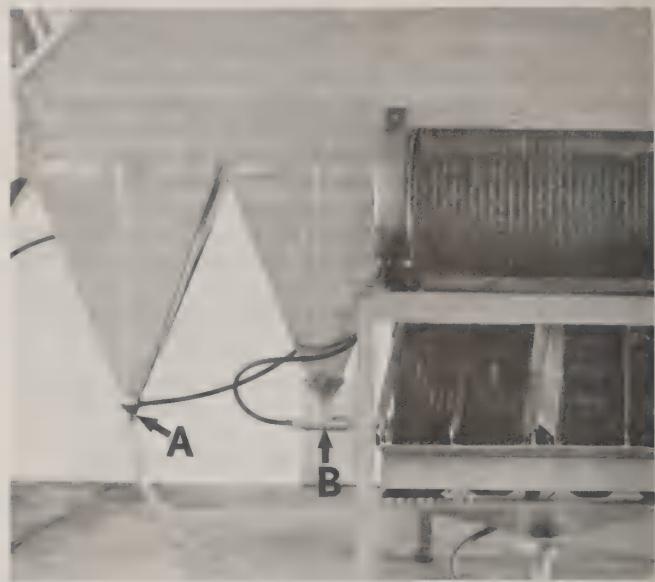Figure 5. Diagramatic longitudinal view illustrating the components of a venturi power head.

Figure 6. Combination use of power heads used in debearding or dehulling. (A) Ring-jet amplifier can be used to convey finished product to the seed bag following seed modification by (B) venturi type power heads.

Air-Seed Separation and Momentum Discrimination

It is first necessary to remove the air from the accelerated seed material for effective, seed-quality classification by momentum discrimination. The more efficient skewed 'Coanda' jet principle (fig. 7) has proved superior to the cross air flow diversion principle previously used in our system.
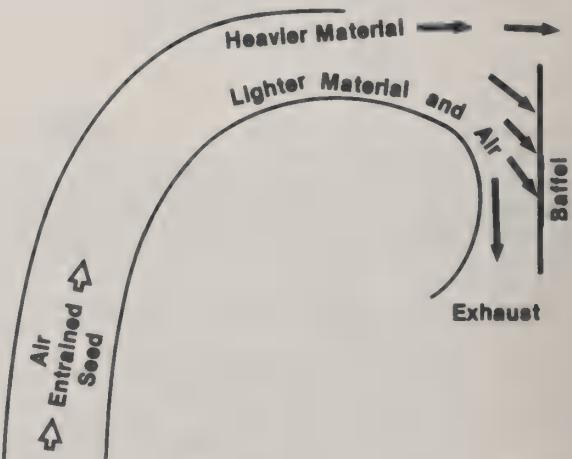

Figure 7. Diagramatic cross section of the skewed 'Coanda' jet principle used for separation of air from the seed.

280

Skewed Coanda Jet

The forcing of air-entrained seed through a curved
tube results in movement of the heavier seed
material along the outer (upper) surface, whereas
air tends to follow the inner (lower) curved
surface due to reduced pressure. In this manner
air is diverted away from the direction of seed
travel allowing the seed material to travel for-
ward on its own momentum.

Momentum Discriminator

The momentum discriminator uses the principle of
inertia to separate seed material by density
classes. High-quality seed is heavier than chaff
or low quality seed and therefore, travels
further by momentum. A momentum discrimination
chamber (fig. 8) eliminates outside air inter-
ference and funnels the seed into various quality
classes as desired.

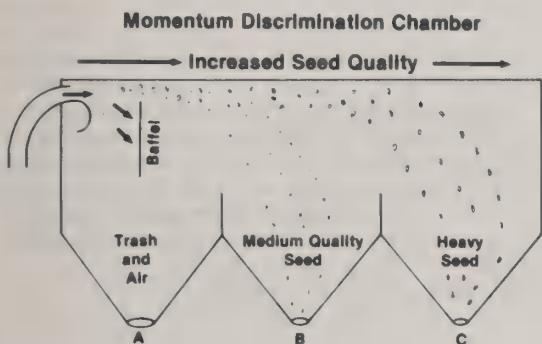**Momentum Discrimination Chamber**

Figure 8. Diagram of momentum discrimination
chamber used for seed quality classifi-
cation. Chamber exit (A) removes
trash and air (dust control), Exit
(B) recycles medium quality seed for
reclassification and chamber exit (C)
removes high quality heavy seed ready
for bagging.

DUST CONTROL

Chaffy seed conditioning by any method will
generate a great deal of undesirable air contami-
nation which is hazardous and uncomfortable to
the operator. This problem can be minimized by
the use of ring-jet amplifiers to move dust away
from the operation. A 25-mm RJA is effective in
taking the dust along with the seed material from
the high intensity scalper to the momentum
discrimination chamber. A 100-mm RJA (fig. 9)
is used to pull the air and dust from the
momentum discrimination chamber away from the
area of operation. Power requirements for dust
control are as great or greater than that of any
function within the conditioning system but seems
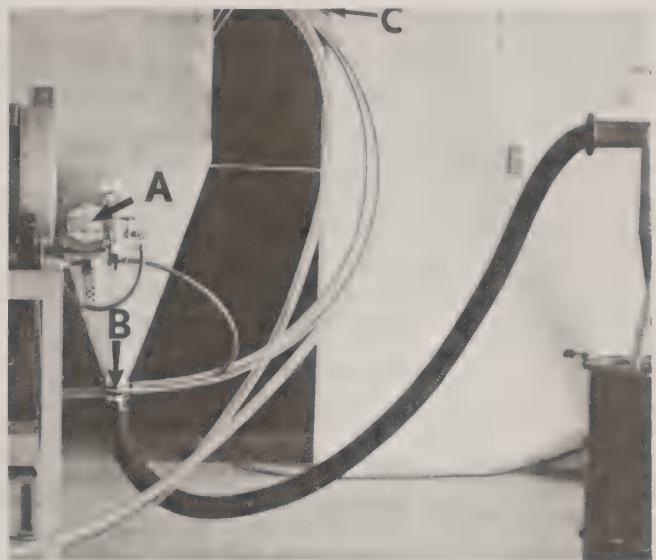justified from a health, safety and comfort
standpoint.

Figure 9. New concepts combined in the 'Woodward
chaffy seed conditioning system'. (A)
pneumatic, right-angle gear motor
(rotary vane type) controls speed of
chaffy seed dispensing, (B) dust con-
trol and (C) curved tubes for air-seed
separation (Coanda jet principle) of
a three module unit.

QUALITY MONITORING

An essential part of the 'Woodward Chaffy Seed
Conditioning System' is a rapid method to
determine seed quality at various points within
the system. The 'Woodward Laboratory Air-Seed
Shucker' (fig. 10) (Beisel, 1985b) is used to
extract grain from seed material to determine
the percent pure grain at any stage within the
operation. This helps eliminate seed losses and
is a useful guide to determine operating speeds
and pressures needed for optimum separation of
seed quality classes. The 'Woodward Laboratory
Air Seed Shucker' can dehull a 5-gram sample of
most chaffy seed and extract the grain in less
than one minute.

MODULAR CONCEPT

Each high intensity scalper including the
tumbling, seed-material dispenser and attached
ring-jet amplifying power head is considered as
a single module unit. One momentum discrimina-
tion chamber can be used for one to several
module units. The pneumatic driven components
operate on a total of 0.45-0.91 m^3/min air volume
depending on the desired speed of tumbling, the
intensity of scalper deck oscillation, and volume
of air required to entrain, convey and accelerate
the amount of seed material being fed from the
scalper into the aerodynamic system. Power
requirements for each module will vary from 5 kW
to 7.5 kW depending on the total air volume
required. Air pressure and volume requirements
for air-driven components of the 'Woodward Chaffy
Seed Conditioning System' are given in Table 1.

Table 1. Minimum and maximum air pressure (kPa) and air volume (m^3/min) required to operate various components of the 'Woodward Chaffy Seed Conditioning System'.

Component	Air Pressure		Air Volume	
	minimum	maximum	minimum	maximum
	kPa	kPa	m^3/min	m^3/min
Mechanical Classification				
Tumbling Seed Dispenser	---	---	.11	.23
High Intensity Scalper	83	276	.17	.34
Aerodynamic Classification				
Power Unit (32 mm RJA)[1]	276	620	.17	.34
Dust Control (100 mm RJA)	138	620	.23	.45
Aerodynamic Seed Modification				
Venturi Power Unit (3.2 mm Nozzle)				
Dehulling (9.6 mm Barrel)	483	827	.57	.85
Debearding (16 mm Barrel)	276	414	.34	.48

[1]RJA = Ring-Jet Amplifier

High quality seed output from a single module will vary from 5 to 30 kg/h depending on the quality and nature of the starting material. Some operators may only need one module whereas operators handling large volumes may use two, three or four depending on quantity of output desired. A 37 kPa diesel driven air compressor will supply all the air needed to run four modules including dust control.

CONCLUSION

The quality of chaffy seeded grasses can be greatly improved with the use of the 'Woodward Chaffy Seed Conditioning System'. Conversion from electric-motors to pneumatic drives increased the range of speed adjustments on mechanical components resulting in greater capacity as well as higher quality seed. The addition of ring-jet amplifiers for seed entrainment, conveyance, and acceleration increased the efficiency of quality classification. Dust control has been built into the system for safety and comfort of the operator, and the modular concept allows flexibility to fit the size of the operation. The 'Woodward Laboratory Air-Seed Shucker' is a valuable component of the system for monitoring quality control.

LITERATURE CITED

Beisel, V. A. 1985a. Sonic seed dehulling system. United States Patent Office. Pat. No. 4505196, March 19, 1985. 4 p.

Beisel, V. A. 1985b. Grass seed from stem remover. United States Patent Office. Pat. No. 4533469, Aug. 6, 1985. 4 p.

Dewald, C. L., V. A. Beisel, and S. Cowles. 1983. The Woodward chaffy seed conditioning system. In Proc. Range and Pasture Seeding in the Southern Great Plains. Texas A&M Univ. Agr. Res. Ctr. Vernon, TX. pp. 69-80.

Woodward Laboratory Air Seed Shucker

A. Venturi nozzle
B. Air-seed impact area
C. Venturi barrel
D. Chaffy seed entrance-dehulled seed exit
E. Classification tube
F. Recycling tube
G. Cyclone dust separator
H. Air exit

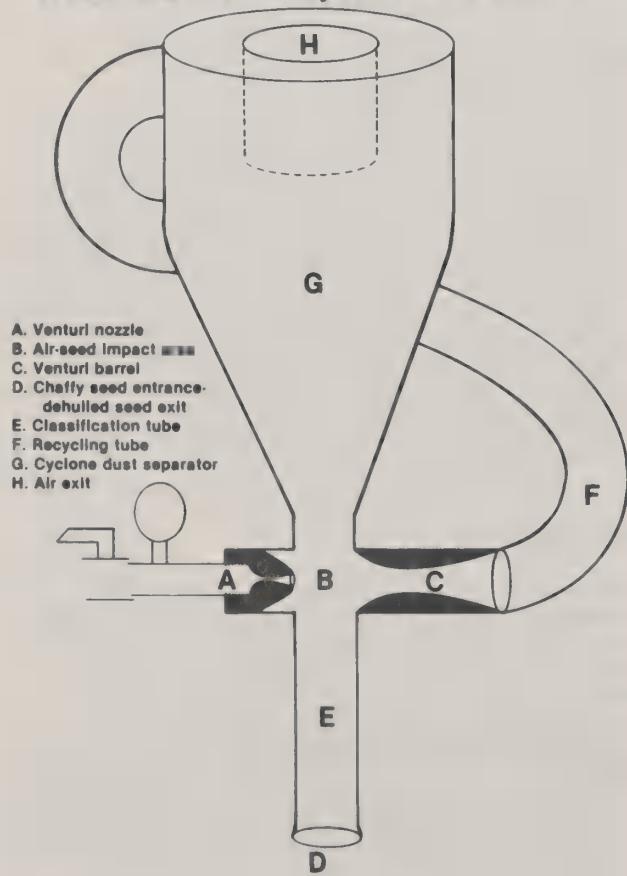Figure 10. Diagram of the 'Woodward Laboratory Air-Seed Shucker' with component parts used to monitor quality control.

INTEGRATION OF MECHANICAL CONTROL OF UNWANTED
PLANTS AND SEEDING EQUIPMENT

Carlton H. Herbel[1]

ABSTRACT

This paper discusses principles and practices
of mechanical control of unwanted plants and
seeding rangelands, and how some practices are
innovatively combined. Seeding methods
discussed are use of rangeland drills, press
drills, grain drills, trashy seed drills,
broadcasting, one-way disk plow, arid-land
seeder, chaining, the land imprinter, and range
interseeder.

INTRODUCTION

Man is making tremendous advances in many
fields of science. We are obtaining increased
productivity from all our agricultural lands,
including rangelands, because of our expanding
needs. Increasingly, people have been able to
influence their environment. A good example of
altering the environment on rangelands is the
use of mechanical methods of brush management
to prepare a seedbed. It is helpful to use a
model to elucidate the practices used in range
management (fig. 1). Sometimes, drastic
manipulations of range ecosystems are needed.
The encroachment and increase of unwanted
plants, the past abuses of people and their
improper use of grazing or fuelwood, or the
desire by the operator to change botanical
composition on all or part of the range unit,
result in practices to control unwanted plants
and to revegetate with desirable plants. These
practices require great attention to detail.
The risk in using plant control or revegetation
is high because, even if attention is given to
every detail, the weather may adversely affect
the desired results. The relative costs of
these practices are high and the potential
benefits are high. Control of unwanted plants
and revegetation may increase herbage
production by 500-1,000 percent or more within
1-3 years. High management inputs are required
because, if these risky, costly practices are
used, the manager should attempt to maximize
the outputs while maintaining the resource, and
minimize the need to repeat the practice.

Few, if any, land managers use intensive
practices exclusively on a unit of rangeland.
Rather, some combination of both intensive and

[1]Supervisory Range Scientist, USDA-ARS,
 Jornada Experimental Range, P.O. Box 3JER,
 NMSU, Las Cruces, New Mexico 88003 in
 cooperation with New Mexico Agricultural
 Experiment Station. Review paper SP279,
 Agricultural Experiment Station, New Mexico
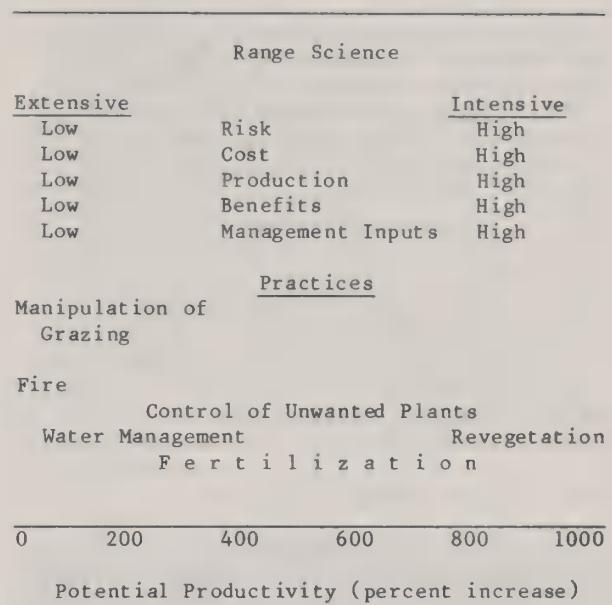 State University, Las Cruces, New Mexico.

Figure 1.   A model of range science (from
           Herbel 1983).

extensive programs are utilized. After a risky
and costly practice, such as revegetation, it
is important to use proper management
techniques to maintain or improve desirable
plants. The use of practices is changing with
time as dictated by economic, political, and
social conditions, or as improved technology
becomes available. Land managers, and others
working with land managers, must be flexible
and innovative in planning operations on a
range unit. What will work well on one range
unit may not work as well on a nearby range
unit (Herbel 1983). The purpose of this paper
is to discuss mechanical control of unwanted
plants and revegetation.

CONTROL OF UNWANTED PLANTS

Plant control in range management involves
reduction of unwanted or undesirable plants
that have invaded or increased in a plant
community. Migration of certain species out of
their normal habitat is one of the major
problems on rangelands of the arid and semiarid
regions. Each species or plant association has
its habitat range to which it is confined. The
environmental factors in a given habitat type
favor certain plant species and plant
associations. This has the effect of confining
the favored species and associations to the
habitat type and rejecting others. This,
however, is true only in an undisturbed
situation.

Plant species or plant associations are
released from their habitat restrictions by

reducing the adjoining, better adapted species or plant associations. This reduction or elimination of competition can be brought about by continued disturbance. The more common disturbances are change in the frequency of fire, drought, and continual and excessive harvesting. The greatest and fastest change can be caused by a combination of two or more factors. For instance, drought in conjunction with excessive harvesting has been a leading disturbance factor in many areas of the world.

Control of unwanted plants allows a more favorable soil water regime for the growth of desirable vegetation. Plant control may be accomplished by chemical, biological, or mechanical means; by judicious use of fire; or by use of certain animal species.

Principles of Mechanical Control

The method selected for mechanical control of unwanted plants depends on a favorable cost, the availability of equipment, the size and stand of the plants to be controlled, whether the target plants have sprouting or nonsprouting characteristics, soil conditions, and the terrain. Herbel (1983) elucidated the principles of mechanical control.

1. Size and stand of the target plants. Rootplowing or disking is used when there is a sparse stand of desirable plants and revegetation is needed. Properly done, rootplowing kills most plants while disking kills nonsprouting plants. Disking is limited to small plants. Chaining is more effective in controlling even-aged, mature shrubs or small trees with stem diameters of 8 cm or more. Bulldozing is effective on sparse stands and medium-sized shrubs or small trees with a stem diameter of about 25 cm.

2. Sprouting or nonsprouting shrubs. Chaining or disking do not kill many shrubs that sprout below the surface of the ground.

3. Soil conditions. Chaining is most effective in areas with lighter-textured sandy or loamy soils. Bulldozing, rootplowing, and disking excessively disturb the soil surface, destroy most plants, and may result in soil erosion. Most mechanical methods cannot be used when the soil is excessively wet. Large rocks also hinder mechanical methods. Generally, shallow soils do not have the production capability to justify the expense associated with mechanical control.

4. Topography. Some mechanical methods leave the soil bare, unprotected, and subject to erosion. There should be a minimum of drainages so equipment can operate at a relatively high speed. Therefore, most mechanical equipment should be used on relatively level terrain.

Some Practices in Mechanical Control

From the rudimentary spike drag implements used to control sagebrush (*Artemisia* spp.) to the more advanced tree crushing equipment used to control juniper (*Juniperus* spp.), there have been many approaches to mechanical plant control because of the widespread variations in climate, topography, and woody species.

Brush Cutters

These implements resemble a stalk cutter used on cultivated crops, but they are much heavier (fig. 2). The use of two sections pulled in tandem with angular alignment between the two units allows for greater crushing and cutting effect. Brush cutters of this type have limitations for range work. Best kills of nonsprouting species are obtained on mature stands of plants of about the same age and size.

Figure 2. Brush cutter on a site infested with big sagebrush (*Artemisia tridentata* Nutt.) in northern New Mexico.

Chaining

Chaining has been used most successfully to control nonsprouting juniper and sagebush. Chains with links weighing over 30 kg are recommended (fig. 3). The advantages of this method are 1) large areas can be treated at a relatively low cost, 2) desirable herbaceous plants are not seriously damaged, and 3) debris and trash protect the soil from erosion. Limitations are 1) many small or supple shrubs and trees are not killed and 2) undesirable herbaceous plants and sprouting shrubs are only slightly damaged (McKenzie et al. 1984). An improvement on the chaining method for some sites was realized by welding disk blades to

Figure 3.   Chaining big sagebrush in northern New Mexico.

A rootplow is a horizontal V-shaped blade that a large track-type tractor pulls underground through the soil, severing plant roots in its path.   Fins are attached to the blade and angled upward so plants are pushed up and out of the soil (fig. 5).   It is one of the few implements capable of controlling dense stands of shrubs that regrow with vigor if only their tops are cut.   It is an effective implement, often killing 80-100 percent of the vegetation and, because of this, the site must be seeded to reestablish desirable species.   For lasting improvements, rootplowing is usually followed by something to prepare the seedbed: for example, fire, the land imprinter, or the arid-land seeder.   A major limitation of the rootplow is that it is ineffective on rough, rocky soil.
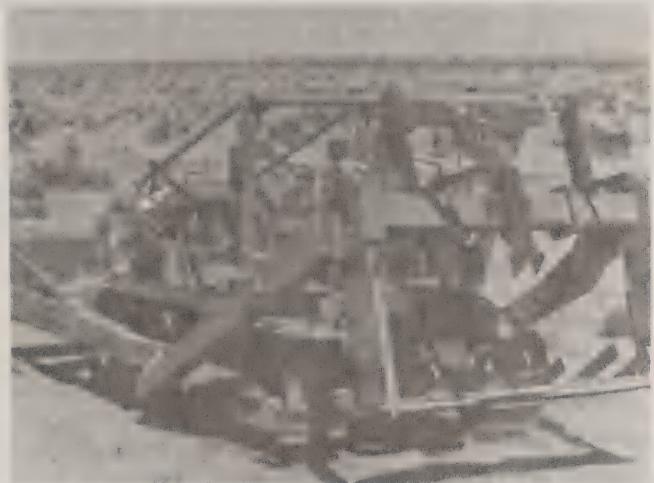
alternate links of a large anchor chain (Wiedemann et al. 1985).   When pulled on a diagonal between two track-type tractors, the disk-chain performs like a giant one-way plow and can traverse heavy brush without difficulty.   The disk-chain may cover extensive acreages and, combined with seeding, is a practical method of vegetation conversion.

Dozing

Pushing with a bulldozer is suited to light stands of trees (<500 stems/ha) (fig.4).

Figure 5.   A rootplow with seven fins to uproot shrubs.

DIRECT SEEDING

Direct seeding can speed range rehabilitation but is expensive, can't be used in all situations, and it is risky.   In deciding whether an area should be seeded, the range manager should ask the following questions:

1.   Is seeding needed? Ranges can often be rehabilitated at a lower cost by improved livestock distribution, better systems of grazing, or reduced stocking rate.   Sometimes, managing unwanted plants results in a dramatic increase of desirable species.   Only where desirable plants are almost completely eliminated is seeding essential.   Such areas will have a range condition rating of poor or low fair.   Where the range condition rating is high fair or better, a range will generally improve with proper grazing management and control of unwanted plants.

Figure 4.   Bulldozing junipers in central New Mexico.

2. Are proven revegetation methods available for the site? Where methods are not available, projects should not be undertaken until acceptable procedures have been developed. On many sites, the procedures are known for the general type but cannot be applied because excessive rocks, steep slopes, or other factors prevent use of the methods needed.

3. Can the area be given proper grazing management after seeding? Seeding should not begin until proper grazing management can be assured. Many seeding failures are caused by improper grazing techniques.

Principles of Seeding Rangeland

Where desirable vegetation has been severely depleted by past grazing abuses, severe droughts, or encroachment of unwanted plants, natural recovery may require several years, or may never occur. Other objectives of seeding are to improve soil stability and to alter plant composition to meet the user's objectives. Seeding rangelands is often a difficult undertaking because of limiting climatic, soil, or topographic features. Herbel (1983) outlined the principles of seeding as:

1. Change in plant cover must be necessary and desirable. Seeding is an expensive and risky undertaking, and should be avoided if possible. However, at least 1 shrub and 10 desirable herbaceous plants per 9 m^2 should be present after revegetation.

2. Terrain and soil must be suitable for seeding. Deep, fertile soils on level to gently sloping land are preferred sites for seeding. Shallow or rocky soils seldom have the potential to justify expensive reclamation measures. Excessive amounts of soluble salts in the soil often require additional attention to ensure adequate plant establishment.

3. Precipitation and water concentration must be adequate. Average annual precipitation, or equivalent from water concentration, must be adequate for germination, seedling growth, and establishment and survival of seeded species. This depends on temperatures but, in temperate climates, a minimum of 250 mm of precipitation may be needed. Where precipitation is near this minimum, only the more drought-resistant species should be used. Existing vegetation is a good indicator of the moisture situation.

4. Remove or reduce competition from unwanted plants. Most plants used for revegetation are perennials. Seedlings of these species are often slow-growing and compete poorly with existing, unwanted plants. A good seedbed will provide the best possible moisture conditions for germination and plant growth. This requires control of most existing plants before seeding. In addition, it is sometimes necessary to control unwanted plants that are competing with seedlings of desirable plants.

5. Use adapted plant materials. Plant species selected for seeding must be compatible with management objectives (e.g., palatability and growth period). It is important to use only those species and varieties well adapted to the soil, climate, and topography of the specific site being revegetated. If native species are chosen, seed from local origin should be used. Local origin would include species from about the same elevation, and within 320 km north, east, or west, and 480 km south of the area to be seeded. Improved ecotypes, varieties, and introduced species may be available for revegetation and should be used.

6. Mixtures of plant types versus single species. The danger in a monoculture seeding is that a disease or insect infestation can eliminate the one species but, in a mixture, some species are likely to survive. Where a variable terrain exists, mixtures will have some survivors on most sites. A variable ground cover will generally result in superior control of soil erosion. Also, mixtures of grasses, forbs, and shrubs will better meet the multiple needs of livestock and wildlife. However, a management problem with multispecies revegetation is that different species often have differing degrees of palatability and differing times of readiness for grazing.

7. Use seed treatments. Various microbial treatments, e.g., nitrogen-fixing bacteria or mycorrhizal fungi, may enhance seedling survival. Dormancy of most seeds can be reduced by stratification -- subjecting them to temperatures 0-4 C for 6-20 weeks in moist sand, peat moss, or newspaper. For some shrubs, treatment with thiourea, or scarification with sulfuric acid or mechanical abrasion, helps overcome dormancy.

8. Use proper seeding rates. It is important to use enough seed to get a good stand, but not more than necessary. Too much seed can produce a stand of seedlings so thick that individual plants compete with each other. Species of plants, number of pure live seeds (PLS) per kg, and potential productivity of the site are major factors determining the seeding rate. PLS is determined by multiplying the germination of a lot of seed by its purity. Seeding rates providing 125-250 PLS/m^2 should be used when the seed is placed in the soil with a drill. Broadcast seeding is not efficient and not an effective method of revegetation because seeds are left on the soil surface and establishment is tenuous. On steep slopes or sites inaccessible to ground traveling equipment, it may be necessary to broadcast. In this case, a doubled seed rate

of 500 PLS/m^2 is recommended.

9. Use the proper seeding depth. Proper seeding depth is determined by the plant species. Optimum seeding depth is roughly 4-7 times the diameter of the seed. Seeding equipment should be used that provides positive seed placement at the desired depth. More stands are lost because seeds are planted too deep, rather than too shallow.

10. Correct seeding time is important. The most desirable time to seed non-irrigated areas is immediately before the season of the most reliable rainfall, and when temperature is favorable for plant establishment.

11. Distribute the seed. Uniform distribution of seed is essential. Skips and missed strips should be avoided. Seeding equipment must be checked frequently to assure it is working properly and not plugged.

12. Alter the microenvironment. Many areas are deficient in soil water for germination and seedling establishment. In some areas, an associated treatment is needed to reduce high soil temperatures and provide more soil water by practices such as mulching, summer fallow, establishing basins, or pits. Intermediate pits, 15 cm deep, 2 m long, and 1.5 m wide were superior for plant establishment to smaller conventional pits, larger bulldozer pits, and an unpitted check in southern Arizona (Slayback and Renney 1972). Reducing soil temperatures can improve seedling establishment in a hot, arid environment (Herbel 1972a). Providing a layer of dead shrubs will reduce soil temperatures. Concentrating water with various land-forming procedures does not always ensure seedling establishment (Herbel 1972b). Surface soil dries rapidly in hot, arid and semiarid areas. This may form a heavy crust on medium- to heavy-textured soils. If the surface can be protected to reduce evaporation, seedling emergence and establishment will be greatly enhanced. Mulches should be considered for plant establishment in difficult environments. The Arid-Land Seeder (fig. 6) was developed to solve the seeding problems discussed above (Abernathy and Herbel 1973, McKenzie and Herbel 1982).

13. Seedbed preparation is essential. The major objectives for preparing seedbeds are 1) remove or substantially reduce competing vegetation, 2) prepare a favorable microenvironment for seedling establishment, 3) firm the soil below seed placement and cover the seed with loose soil, and 4) if possible, leave mulch on the soil surface to reduce erosion and to improve the microenvironment. We should not expect a comparatively weak perennial seedling to become established under conditions where a stronger annual seedling has difficulty or cannot live.
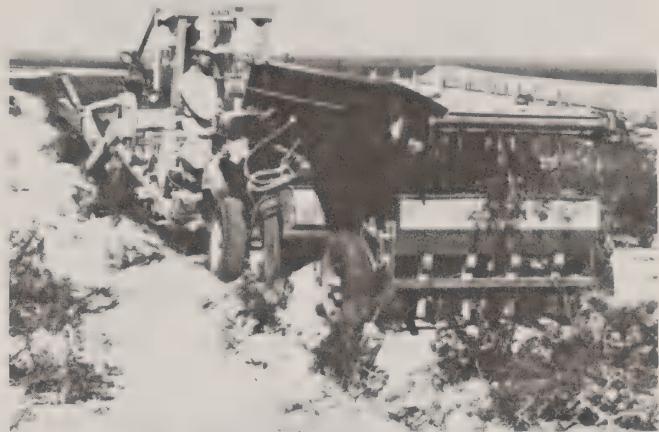

Figure 6. The Arid-Land Seeder concentrates water and seeds, and places a mulch of dead shrubs over the seeded area.

14. Fertilization. Where water is not limiting, a nitrogen-phosphorus plant fertilizer applied in bands near the seed zone may help plant establishment.

15. Revegetated areas must be properly managed. All seedings must be protected from grazing animals through the second growing season, or until the seeded species are well established. Under certain conditions, spraying to control weeds competing with the new seedlings can prevent the loss of a seeding. Rodents, rabbits, insects, and other pests should also be controlled where they are a menace to new seedings.

Methods of Direct Planting

Direct planting can be done with a rangeland drill, press seeder, grain drill, range interseeder, browse seeder, aerial broadcasting, rotary spreader, airstream, hand broadcasting, or by other methods that take into consideration range seeding principles.

Drill Seeding

Drilling is by far the superior method of planting seed where site conditions permit. The seed is covered to the proper depth by the drill control; distribution is uniform; rate of seeding is positively controlled; and compaction can be applied if needed. There are several types of drills available (Larson 1980).

Rangeland Drill. This drill is a rugged seeder with high clearance designed to work on

rough sites (fig. 7). It has performed well on rough seedbeds. It can be converted to a deep furrow implement by removing the depth bands. The disks are cupped enough to make good furrows. The furrow depth is controlled by addition or removal of disk arm weights. Weights up to 30 kg have been used under some conditions. The feed on this drill will not handle trashy seed unless the feeder is especially designed for that purpose (Young and McKenzie 1982).

Figure 7. Rangeland drill equipped with seedboxes for small seed and for chaffy seed.

Press Drill. The press drill is designed for seeding on plowed or loose seedbeds. A heavy press wheel packs the soil. The seed is placed in the packed furrow and an adjustable drag covers the seed (fig. 8). This drill
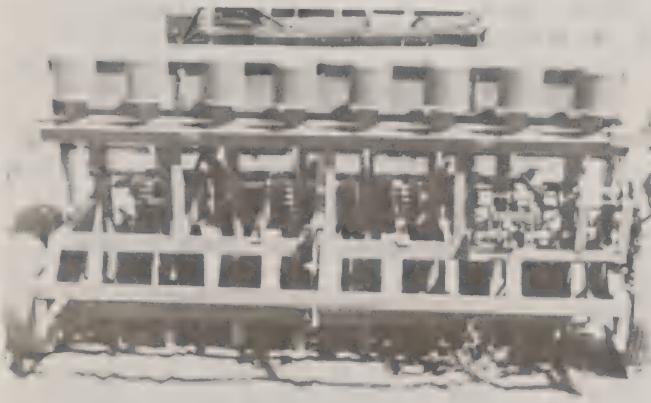

Figure 8. A press drill.

cannot be used on rocky or rough seedbeds. Trashy seed can go through the feed on this drill if it is designed for this purpose.

Ordinary Grain Drills. Grain drills are designed and built for use on cultivated fields. They are often too lightly constructed for rough rangeland seeding. Breakage is a problem and the seed may not be placed properly in the ground. For these reasons, they have limited use for critical area seedings.

Trashy Seed Drill. This drill is equipped with two types of seed boxes, one for planting trashy seed such as buffelgrass (*Cenchrus ciliaris* L.) and another for planting fine seeds, such as lovegrasses (*Eragrostis* spp). Both boxes can be used together or separately. The drill has a welded frame construction and uses rubber-tired wheels.

Broadcasting

Broadcasting is any method that scatters the seed directly on the soil without soil coverage. However it is spread, the seed must be covered in some way if it is to germinate and become established. Size of seed and condition of the seedbed are important factors influencing seed coverage with soil. A seedbed that is 5-8 cm of loose soil generally sluffs sufficiently to cover the seed. Covering the seed with a mulch is better than no coverage at all, but mulch coverage is not as good as soil coverage. If mulches are used in conjunction with seeding, best results are obtained by broadcasting the seed, covering with soil, and applying mulch. Limitations to broadcast seeding are 1) heavy seeding rate is required, 2) covering of seed is poor compared to drilling, 3) distribution of seed is often poor, 4) loss of seed to insects and rodents can be great, and 5) establishment is generally slower. This method should be avoided if possible. Some means of obtaining seed coverage include dragging a chain (chaining), raking with a hand implement, or driving a vehicle or livestock over the area after scattering seed.

Aerial Applications. Aircraft must be equipped with a positive, power-driven, seed metering device. An adjustable opening that allows the seed to drop out of the hopper by gravity is not acceptable when a mixture of various seed sizes and weights is being seeded.

Broadcasting Ground Application. Ground broadcasters are primarily of three types.

- Rotary spreaders. In this type, the seed falls from a hopper into a rotating, ribbed disk that distributes the seed by centrifugal force. The width of throw depends on size and weight of seed, speed of the rotating disk, and velocity of wind. Rotary

spreaders may be carried by hand, mounted on a tractor or seedbed preparation unit, or trailed behind. They are usually powered by hand, gasoline or electric motor, or power take-off.

- Seeder boxes of the drill-like or fertilizer-spreader type. In this type, a fluted or forced gear-fed mechanism lets seed fall out of the bottom of the box onto the ground. The seedbox is mounted on equipment such as brushland plows or brush cutters. In general, the seeder box type of broadcaster distributes seed more uniformly than does the rotary type.

- Dribblers. A recent adaptation of this type of broadcaster is the seed dribbler. The dribbler was designed to be mounted on the right and left side of the deck of a track-type tractor. The seeddrop mechanism has a direct drive from a rubber-tired wheel riding on the tractor tracks and utilizes a fluted forced feed. The seed is metered onto the track pad just as it breaks over the front idler. It drops off the pad in front of the track and is embedded in the soil as the tracks pass over.

- Broadcast units using an air stream to dispense seed. The seed is metered from a hopper, either by gravity or forced gear, into an air stream. The air stream can be created either by exhaust from equipment motors or by a fan designed for this purpose. Seed distribution is poor when wind velocities are high. Swath width is unpredictable, depending on weather conditions.

- Ground application by manual equipment. This method is as old as civilization; the Bible speaks of such methods. Many small areas are still seeded by a sower throwing seed from a sack suspended at a person's side with a shoulder strap. An experienced person can maintain a good distribution of seed by this method.

An adaptation of manual seeding is the Whirlwind seeder. This hand implement consists of a canvas seed container with a controlled feed that drops seed on a disc. A crank is turned by the sower as he walks, and the crank gear turns the disc. The spinning action of the disc scatters the seed. This method is often used after bulldozing or other spot treatment that removes existing plants.

COMBINING MECHANICAL CONTROL OF WEEDS WITH SEEDING

Normally, mechanical weed control and rangeland revegetation requires consideration of the principles described above. As mentioned previously, some operations are combined to remove brush, prepare the soil, and sow the seed. The one-way disk plow with seedbox has been used on large areas to control big sagebrush (*Artemisia tridentata* Nutt.) and seed

crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] (Cornelius and Talbot 1955). The arid-land seeder combines a rootplow, a conveyor, a hydraulically-operated dozer blade, and a press-wheel seeder to control brush such as creosotebush [*Larrea tridentata* (Sesse & Mocino ex DC.) Coville] and tarbush (*Flourensia cernua* DC.), form basin pits to hold precipitation on the seeded area, seed a variety of species, and use the dead brush as a mulch on the seeded area (Abernathy and Herbel 1973).

Chaining, diskplowing, and rootplowing reduced brush competition at three sites in southeastern Arizona (Jordan 1968 as cited in Cox et al. 1982). Each treatment was pitted and sown to Lehmann lovegrass (*Eragrostis lehmanniana* Nees). Lehmann lovegrass was established with all treatments, but density and production rapidly declined unless the treatment included rootplowing.

The land imprinter is another innovative mechanism that attempts to combine some of the principles of mechanical weed control and seeding. The land imprinter is a hollow metal cylinder, 1 m in diameter and 2 m long pulled by an ordinary farm tractor (fig. 9). The cylinder surface has V-shaped ridges that leave imprints up to 10 cm deep in a furrow, making an indentation pattern that keeps rainwater where it falls. These imprints provide a small water and litter catchment capable of storing sparse rainfall. The cylinder can be filled with 2 tonnes of water to increase imprinting pressure when used on more resistant soils. A variety of imprinting patterns are available offering flexibility for working with different soils, terrains, and climatic conditions. Seeding is done by an inexpensive broadcast-type seeder mounted on the tractor, or on the towing tongue of the imprinter, which allows the imprinter being towed to press the seed

Figure 9. A land imprinter.

into the soil. The basic imprinting pattern creates a runoff groove that channels water to the seedbed groove where germination and plant growth can occur, even under less than normal rainfall. The machine rolls over and crushes brush, including individual plants with a basal diameter of up to 10 cm, although its best effectiveness is on stems less than 5 cm in diameter. Destruction of dense, old brush is not as effective as more specialized machines designed specifically for total brush removal; however, some brush is effectively killed, and the remainder is sufficiently damaged to delay regrowth until after the critical period for successful establishment of the new grass seedlings. At that time, the recuperating brush encounters strong soil water and nutrient competition from the seeded species. The land imprinter has the added benefit of mulching existing vegetation into the soil to help retain moisture, provide soil aeration, and contribute to soil structure and nutrients. When the land imprinter is operated on dry soil, crushing stems into the soil is less effective than on moist soil.

Range interseeding increased productivity and the proportion of desirable forage species on depleted ranges of the northern Great Plains (Houston and Adams 1971). The principle of range interseeding is to seed in a scalped furrow that has all vegetation removed from it. The furrows are prepared by undercutting about 5 cm below ground level and placing the sod strips to the side of the furrow. The width of the furrow, usually 25-45 cm, is important to seeding success through reduction of competition for soil water. An interseeder that prepares furrows 12-20 cm wide was developed in South Dakota (Chisholm et al. 1981). Wider furrows are desirable in arid areas.
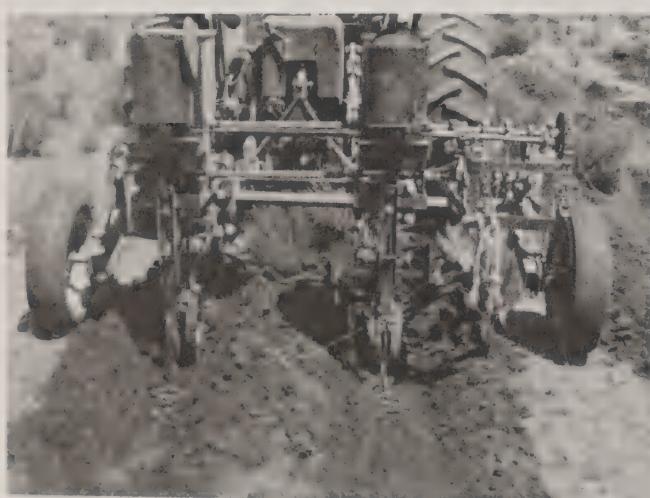

Figure 10. A range interseeder.

CONCLUSIONS

Throughout the rangelands of the world, there are large areas where desirable forage plants have been reduced in vigor or killed by past abuses. Such lands produce few benefits and are a detriment to adjacent lands. Even with controlled livestock grazing and, in some cases, complete protection, depleted areas will require 20 or more years to develop desirable plants. Secondary succession is slow, or non-existent, in arid and semiarid rangelands when the desirable vegetation has been depleted. Mechanical control of unwanted plants may be used to manage undesirable species and prepare a seedbed. If propagules and desirable plants have been depleted, revegetation is the only means to establish plants for protection and production.

LITERATURE CITED

Abernathy, G. H. and C. H. Herbel. 1973. Brush eradicating, basin pitting, and seeding machine for arid to semiarid rangeland. J. Range Manage. 26:189-192.

Chisholm, T. S., F. R. Vigil, T. M. Klosterman, and G. Orcutt. 1981. Interseeding and plans for SDSU's new machine...for better pasture production. S. Dak. Agric. Exp. Sta. B-680. 14 pp.

Cornelius, D. R. and M. W. Talbot. 1955. Rangeland improvement through seeding and weed control on east slope Sierra Nevada and on southern Cascade Mountains. U.S. Dep. Agric., Agric. Handb. 88. 51 pp.

Cox, J. R., H. L. Morton, T. N. Johnsen, Jr., G. L. Jordan, S. C. Martin, and L. C. Fierro. 1982. Vegetation restoration in the Chihuahuan and Sonoran Deserts of North America. U.S. Dep. Agric., Agric. Res. Serv., Agric. Rev. and Manuals, ARM-W-28. 37 pp.

Herbel, C. H. 1972a. Environmental modification for seedling establishment, pp. 101-114. In The Biology and Utilization of Grasses, V. B. Youngner and C. M. McKell, eds. Academic Press, Inc., New York.

Herbel, C. H. 1972b. Using mechanical equipment to modify the seedling environment, pp. 369-381. In Wildland Shrubs--Their Biology and Utilization, C. M. McKell, J. S. Blaisdell, and J. R. Gooden, eds. U.S. Dep. Agric., Forest Serv. Gen. Tech. Rep. INT-1.

Herbel, C. H. 1983. Principles of intensive range improvements. J. Range Manage. 36:140-144.

Houston, W. R. and R. E. Adams. 1971.
    Interseeding for range improvement in the
    northern Great Plains. J. Range Manage.
    24:457-461.

Larson, J. E. 1980. Revegetation equipment
    catalog. Vegetation Rehabilitation and
    Equipment Workshop, U.S. Dep. Agric.,
    Forest Serv., Missoula, Mont. 198 pp.

McKenzie, D. W. and C. H. Herbel. 1982. Arid
    land seeder development. U.S. Dep. Agric.,
    Forest Serv. Spec. Rep. 8222-1802. 6 pp.

McKenzie, D., F. R. Jensen, T. N. Johnsen,
    Jr., and J. A. Young. 1984. Chains for
    mechanical brush control. Rangelands
    6:122-127.

Slayback, R. D. and C. W. Renney. 1972.
    Intermediate pits reduce gamble in range
    seeding in the Southwest. J. Range Manage.
    25:224-227.

Wiedemann, H. T., D. W. McKenzie, and T. V.
    Russell. 1985. Disk-chain for seedbed
    preparation. Rangelands 7:28-30.

Young, J. A. and D. McKenzie. 1982. Rangeland
    drill. Rangelands 4:108-113.

ENGINEERING SEEDING SYSTEMS FOR RESTORATION OF
RANGELANDS

Harold T. Wiedemann[1]

ABSTRACT

Successful seeding depends in part on proper
equipment. A disk-chain developed for rangeland
seedbed preparation is effective and cost
efficient. Chaffy seed metering devices developed
for ground and aerial seeders are accurate and
commercially available. These engineering systems
appear valuable for seeding extensive areas of
rangeland.

INTRODUCTION

Seeding of rangeland with more productive forage
plants has the potential to substantially increase
forage and livestock production, particularly on
the more productive range sites (Fisher et al.
1973). However, the practice has been hampered by
the high cost of land preparation and seeding.
Research was initiated by the Texas Agricultural
Experiment Station in 1972 to develop novel
equipment and more reliable techniques for
rangeland revegetation. Early studies by
Wiedemann and Brock (1975) found that land
rootplowed for brush control is often too littered
with brush debris to revegetate with conventional
equipment. This paper describes successful
developments in the design of innovative equipment
for rangeland seedbed preparation and seeding that
requires a minimum of land cleanup.

ENGINEERING SYSTEMS FOR LAND SURFACE MODIFICATION

Disk-Chain Innovation

Early studies by Wiedemann et al. (1979) on
rootplowed land showed that seedbeds prepared with
a heavy-duty offset disk consistently produced
better grass stands than roller chopping or
chaining, but log-littered land often precluded
its use. To solve this problem, a disk-chain was
developed (fig. 1) to reduce the cost of rangeland
disking and eliminate the need for costly raking
(Wiedemann and Cross 1982). A disk-chain is an
anchor chain with disk blades welded to alternate
chain links. Disking action occurs when the
chain, with swivels attached to each end, rotates
as it is pulled diagonally.

Implement Draft

Field tests were conducted to determine drawbar
draft of disk-chains using a load cell attached to

Figure 1. Disk-chain developed by the Texas
Agricultural Experiment Station for
seedbed preparation of log-littered
rangelands (Wiedemann and Cross 1985b).

the drawbar. Data were collected and processed
using a compact microprocessor with a memory chip
and portable printer (Wiedemann and Cross 1983).
Operating mass per blade for each 20-blade unit
was determined (weight of two chain links and one
disk blade). Penetrometer cone index (CI) values
were determined at each test site to quantify soil
strength. Test procedures are outlined by
Wiedemann and Cross (1985b).

Initial testing determined a disk-chain pulled in
a triangular configuration (fig. 1) reduced draft
by 36%, increased operating width by 23% and
required only one tractor compared to the original
diagonal pulling technique which required two
tractors. All subsequent testing used the
triangular pulling technique.

The optimum disk-chain selected for seedbeds
prepared on rootplowed land (CI = 0.78 MPa)
weighed 33.6 kg/blade (5-cm chain and 61-cm disk
blades). Draft for this unit was 667 N/blade at
4.8 km/h.

Field tests were also conducted on undisturbed,
native rangeland to determine disk-chain
performance for seedbed preparation (Wiedemann and
Cross 1985a). Draft of disk-chains was positively
correlated to operating mass and each additional
kilogram of mass increased draft by 18.2 newtons
of force. Draft was not significantly (P>0.10)
influenced by soil cone index (soil condition).
Thus, the draft prediction equation Y=0.80+18.24M
illustrated in figure 2, which considers only
operating mass (M), is valid over the broad range
of conditions tested. However, both mass (M in
kg) and cone index (CI in kPa) were significant
factors in predicting depth of operation which is
best described by the equation Y=5.7+0.06M-0.0007
CI. Operating depth is illustrated in figure 2
for three soil conditions.
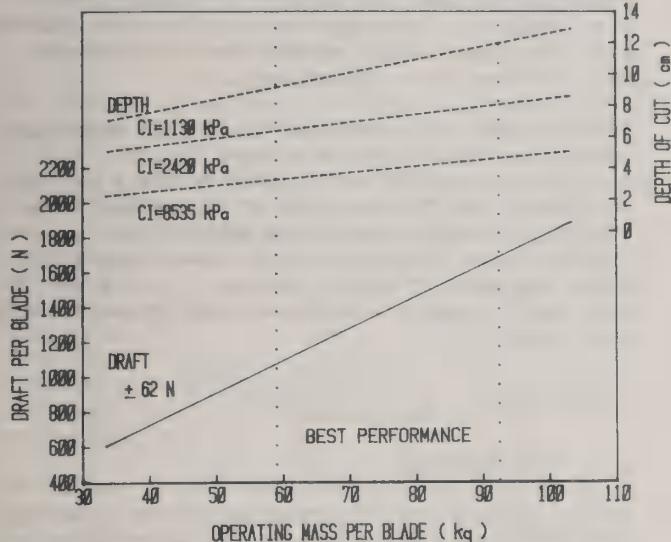
DISK-CHAIN PERFORMANCE

Figure 2. Disk-chain draft and depth of cut when
pulled at 4.8 km/h in native rangeland
soil of various cone indexes (CI in
kPa).

The optimum disk-chain selected for seedbed
preparation on undisturbed native rangeland
weighed 94.3 kg/blade (7.6-cm chain and 61-cm disk
blades). Draft of this unit was 1690 N/blade at
4.8 km/h with a predicted depth of cut of 5.6 to
12.2 cm. Estimated pulling cost for a 20-blade
unit is $14.92/h (140 hp crawler tractor at $65/hr
in 3rd gear [4.8 km/h]).

Development of a flexing roller (vertical movement
only) for the rear, disk-chain brace, figure 3 has
made disk-chains greater than 8 m in width
practical. Our prototype rollers for 20-blade
units were 7.9, 10.2 and 12 m for 4.8-, 6.4- and
7.6-cm chains, respectively. Complete roller
details are available from the USDA Forest Service
(1986).

Vegetative Dynamics

Tests to compare disk-chaining, smooth chaining
and disking alone were installed on rangeland
infested with mesquite (Prosopis glandulosa Torr.
var. glandulosa) (Gould 1975). A clay loam site
was located near Vernon, Texas and a loamy sand
site was located near Guthrie, Texas. Following
rootplowing for brush control, the various
seedbeds were aerially seeded with 1.1 or 2.2 kg
PLS (Pure Live Seed)/ha of kleingrass (Panicum
coloratum). Experimental design was a split block
with four replications at each site. There were
no significant differences in grass densities
between seedbeds prepared by disk-chaining (7.2
plants/m^2) and offset disking (6.9 plants/m^2), but
both were significantly (P<0.05) higher than
chaining alone, (4.7 plants/m^2). In similar

experiments conducted over a three-year period,
seeded grass densities were increased 35 and 92%
by disk-chaining over seedbeds prepared by smooth
chaining in loamy sand and clay loam soil,
respectively (Wiedemann and Cross 1985b).

ENGINEERING SYSTEMS FOR VEGETATIVE MANIPULATION

Ground Seeding Innovations

Uniform metering of chaffy or irregularly shaped
seed from grass drills has been a serious problem
for many years (Brock et al. 1970). In addition,
much of the seeding equipment has been designed
for clean-tilled land and does not withstand the
rigors of rough rangeland. To overcome the
metering problems, a semi-circular seedbox was
constructed to allow an agitator to rotate all
seed in the seedbox. Agitator styles of fingers,
paddles and augers, and pickerwheel widths of 6.4,
12.7, 25.4, 50.8 and 101.6 mm were evaluated using
sideoats grama (Bouteloua curtipendula) seed
(Wiedemann et al. 1979). A combination of the
semicircular seedbox, auger agitator and 12.7 mm
wide pickerwheel with eight teeth gave the best
results. This experimental metering device
resulted in a seeding rate decrease of only 15%
while metering 75% of the seed from the seedbox at
a pickerwheel speed of 10 rpm (fig. 4). This
compares to a seeding rate decrease of 99% before
75% were metered from the seedbox of a standard
Nesbit rangeland drill using a pickerwheel speed
of 30 rpm. The 10 rpm seeding rate of the
experimental unit was found to be comparable to 30
rpm rate of the Nesbit unit. The experimental
unit easily metered 97% of the seed from the
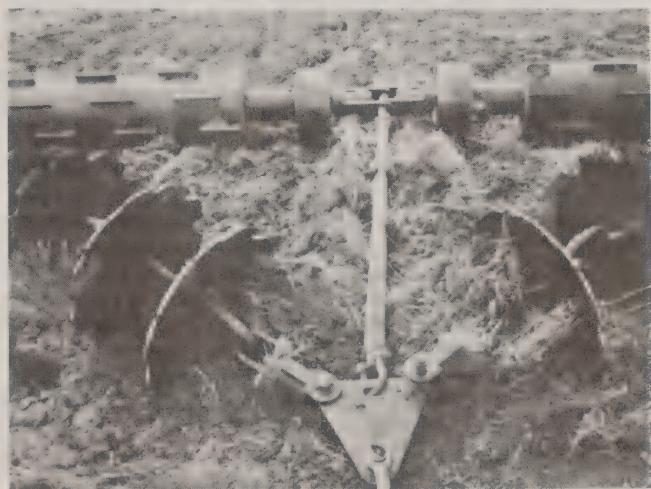seedbox during static test conditions.

Figure 3. Flexing joint in rolling brace of disk-
chain allows vertical movement of roller
when traversing rough land and the rigid
pipe brace assures proper joint
alignment during operation.
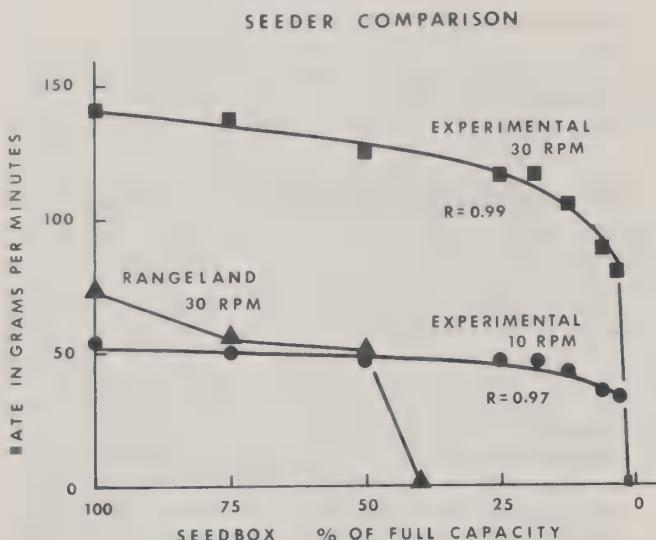
SEEDER COMPARISON

Figure 4. Comparison of uniform seeding rates of the experimental metering device, developed by the Texas Agricultural Experiment Station to the non-uniform rates of a standard rangeland metering device.

Experiments also were conducted with caucasian bluestem (Bothriochloa caucasicus), little bluestem (Schizachyrium scoparius), buffelgrass, (Cenchrus ciliaris), galleta (Hilaria jamesii), fourwing saltbush (Atriplex canescens) and winterfat (Ceratodes lanata). These experiments were outlined by Wiedemann (1982, 1984). The semicircular seedbox with auger agitation dispensed at least 97% of the seed of each species from the box. Seeding rate as a function of the amount of seed in the hopper was predictable with significant r^2 values over 0.90 based on regression analysis. Buffelgrass seed, one of the most difficult to meter, had a decrease in seeding rate of only 33% while metering 75% of the seed from the seedbox.

Early work with seed mixtures demonstrated the need for a separate seedbox to meter small slick seed (Wiedemann et al. 1979). A John Deere[2], double-run, internal cup-feed seeding mechanism functioned well using a variety of slick seed containing limited amounts of trash. A prototype seeder with seedboxes for both chaffy and slick seed was mounted on a heavy-duty frame with flexing runner openers (fig. 5). Field performance of this experimental rangeland seeder has been excellent over five years of testing (Wiedemann et al. 1979). The seeder has operated successfully on seedbeds prepared by chaining, roller chopping or disking following rootplowing

---

[2]Mention of a trade name is for identification only and does not imply an endorsement or preference by the Texas Agricultural Experiment Station over other products not mentioned.

when sparse amounts of logs and stumps up to 30-cm diameters or moderate amounts of lesser debris were present. Seedling densities in areas planted with the experimental seeder were 107% greater than similar areas seeded aerially.

The improved performance of the chaffy metering system has resulted in six grass drill manufacturers adopting the seed metering process which accounts for over 85% of the market. The flexing, runner openers were adopted only on a limited basis because the land owner generally rakes the area if ground seeding is preferred so that drill seeders with double disk-openers can be utilized.

Aerial Seeding Innovations

Seed Metering

Aerial seeding offers a fast method for covering extensive areas of rangeland, but metering of grass seed from aircraft has posed numerous problems. Hard, slick seed flows evenly through the hopper-gate opening only at high rates of seeding. When low seeding rates (1.1 to 2.2 kg/ha) of small slick seed such as kleingrass or lovegrass (Eragrostis spp.) are attempted, metering is erratic because of the very small opening at the hopper gate. A fluted baffel was developed that allows a wider hopper-gate opening (Wiedemann et al. 1980). This design has resulted in considerable improvement in metering; however, precision was not considered adequate. Grass seed chaffier than sideoats grama, such as bluestems and buffelgrass, have not been successfully

Figure 5. Prototype rangeland seeder with experimental chaffy seed metering device and individual hoppers with cup-feed mechanism for small slick seed metering, and flexing runner openers to place seed in the furrow without undue mechanical breakage from logs up to 30 cm in diameter (Wiedemann et al. 1979). Foam-filled tires prevent flats.

metered from aircraft because they bridge the hopper-gate opening causing complete stoppage of seed flow (Hardcastle 1983). The best solution to aerial seeding of chaffy seed apparently is to modify the seed for improved metering characteristics (Wiedemann 1985).

Bluestem seed has been successfully modified for improved metering by Dewald et al. (1983) with a device that uses super, high-speed air to strip the chaff from the caryopsis of bluestem seed. This process appears very promising since the small slick caryopsis can then be accurately metered aerially with a positive metering device researched by Bouse et al. (1982) and commercially developed by Elanco Products [Meterate][3] and Jack Duke [Duke Metering System][4]. The vaned-rotor metering devices were designed for pelleted products and definite modifications are needed for grass seeding, but they show excellent promise for metering slick seed.

Aerial seeding of caryopses must be thoroughly field tested for stand establishment characteristics as well as metering accuracy for the complete system to be successful. Stand establishment of WW Spar bluestem from hulled and chaffy seed is discussed later.

Seed Modification

An "air shucker" developed by Aaron Beisel in cooperation with the USDA-ARS at Woodward, OK, strips appendages from chaffy bluestem seed (Dewald et al. 1983). The seed shucker consists of a power unit (nozzle, mixing chamber and venturi muzzle), recycling tube, cyclone air separator, and classification cylinder (fig. 6). Compressed air (275 to 620 kPa) enters the power unit nozzle and travels through the mixing chamber to exit through the venturi muzzle at super high speed. Air-entrained chaffy seed enter the mixing chamber where the impinging air blast and resulting acceleration force strip the subtending appendages from the grain (caryopsis). Clean grain, because it is more dense than the chaffy seed, falls from the classification cylinder. Seed not shucked on the first cycle, pass from the cyclone air separator and re-enter the venturi muzzle until shucking is completed. The laboratory method is fast (less than a minute cleaning time for 5-g sample) and does not damage the seed as a hammer mill cleaning method can. Cleaning time varies with different species of grass. Commercial units, patented by Aaron Beisel, Fargo, OK, are in high demand for seed quality analytical work because of the increased accuracy and speed of cleaning. Subsequently, a continuous flow unit with a capacity of 25 kg/h

---

[3]Elanco Products Company. A division of Eli Lilly and Company. Product information. 740 South Alabama Street, Indianapolis, Indiana 46285.
[4]Duke, Jack. Duke Metering Equipment Company, Inc. Product literature. 559 Skyland Boulevard, Tuscaloosa, Alabama 34505.

Figure 6. Seed shucker developed to aerodynamically strip chaff from the caryopsis (grain) of grass seed. Components include: A, power unit (nozzle, mixing chamber and venturi muzzle); B, recycling tube; C, cyclone air separator; and D, classification cylinder.

has been developed for commercial seed cleaning. Modifying the chaffy seed reduced the bulk volume (1/bulk density) by 96.7 percent and reduced the amount of bulk seed required by 58.7 percent assuming germination is the same for both seed types, see Table 1. Additionally, the number of seed per unit mass was increased by 80 percent. The use of hulled WW Spar would allow agricultural aircraft to carry a 160 ha load. Flying time would become the limiting factor rather than hopper load.

Table 1. Comparison of physical characteristics of naturally chaffy and hulled seed of WW Spar bluestem.[1/]

WW Spar	Purity	Bulk Density	Seeds per g
	%	kg/m^3	No.
Chaffy	41.3	24.8	1210
Hulled	99.7	752.0	2180

[1/] Purity was determined from 10, 5 g samples. Bulk density was determined from 10, 10 g samples. Seed counts were determined from 100, 0.1 g samples.

Laboratory Metering System

A laboratory model of a positive metering system using the vaned-rotor concept was constructed to quickly screen rotor variables. Design was similar to the final prototype developed by Bouse et al. (1982). Outside diameter of the rotor was 76 mm and vane height was 6, 13 or 19 mm. Each rotor used 12 vanes. The clear plastic gate box and rotor were 15-cm wide. An electrically driven, variable speed drive unit powered the rotor. Flow rates of seed from the 13- and 19-mm vaned rotors far exceeded the desired rates equivalent to 1.1 to 4.4 kg/ha. The required rate of 20 to 60 gm/sec was obtained with speeds of less than 50 rpm from the 6-mm vaned rotor when metering kleingrass.

Flow rates of slick kleingrass and lovegrass were compared to WW Spar bluestem seed cleaned by the air-impinging technique. Coated buffelgrass was used as a reference for metering characteristics of coated seed[5]. The air-modified seed are labeled hulled Spar and are the caryopsis only. Comparison of these grasses dispensed from the 6-mm vaned rotor indicated that lovegrass and hulled Spar would meter similarly (fig. 7). These fine seeded grasses will probably require the addition of a filler such as cracked grain before they can be metered from current commercial units. Kleingrass, with a lower bulk density than hulled Spar or lovegrass, generated a lower output of seed at a given rotor rpm. The large, coated buffelgrass seed resulted in the lowest flow rate. All seed, however, produced a linear relationship between flow rate and rotor speed up to 125 rpm for all grass tested except buffelgrass, which was only tested up to 75 rpm. This linear relationship will greatly benefit field calibration of the system.

Aerial applications

Installations. Aerial seeding studies were installed at five locations using two rates of WW Spar bluestem hulled by the air-impinging device. Aerially seeded plots were 305 by 61 or 122 m, swath width was 15 m, and each study site was approximately 16 ha. The two seeding rates were applied to four different seedbed preparations at each location. Seed lots were weighed before and after each flight to determine amount dispensed. Applications were made with a Cessna Ag-Truck aircraft equipped with a positive metering system and a Transland Slimline spreader. Air speed was approximately 160 km/h. Cottonseed meal was mixed with hulled bluestem seed at a 1:1 w/w ratio to reduce the seed flow rate from the metering rotor. With this mix, rotor speed was sufficient to maintain uniform output while providing the desired low seeding rate.

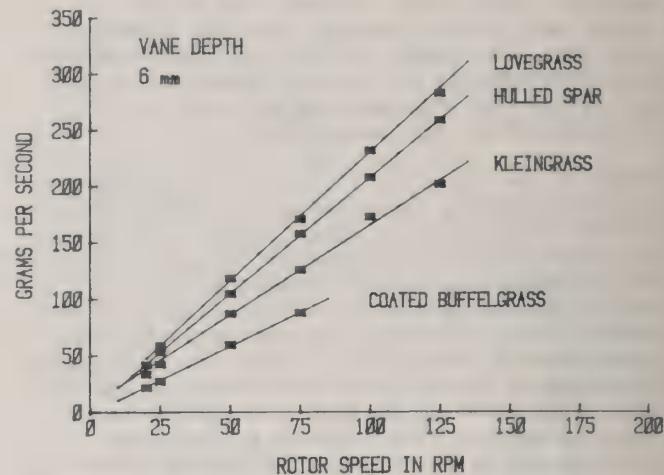[5]Pogue, Gary. Flamecoat. Buffelgrass Seed. Product literature. P.O. Drawer 389, Kenedy, Texas 78119.

Figure 7. Flow rates of seed from various range grasses metered by a laboratory model of a positive meter device with 6-mm vanes (Wiedemann 1985).

Exploratory tests demonstrated that the positive metering system could be satisfactorily calibrated on the ground (Wiedemann 1985). Slight variations could be corrected by adjusting the rotor speed by the same percentage that the actual seeding rate has deviated from the desired rate, see Table 2. Seeding rates after adjustment varied from 0.61 to 0.64 kg/ha for the targeted 0.5 kg/ha rate, and 1.03 to 1.28 kg/ha for the targeted 1.1 kg/ha rate. The seeding rate accuracy achieved in these plots was considered exceptionally good. The average coefficient of variation for 27 plots over a 2-year period was $4.0\% \pm 0.88$ ($\bar{x} \pm SE$). Uniform output of seed could not be maintained at driving motor speeds below 500 rpm. Operation of the system could be improved if the seed dispensing rotor was modified so that motor speeds of 1000 to 2000 rpm could be used.

Timing of Aerial Application. During a five-year study comparing different seedbeds seeded by an experimental drill and standard aerial methods (Wiedemann et al. 1979) it was observed that timing of the aerial seeding in relation to rainfall was critical to seeding success. Results further indicated that disking prior to seeding improved grass stands substantially over other methods. Recent studies conducted over a three-year period showed that broadcast seeding (simulated aerial) on seedbeds crusted by rainfall reduced grass densities in excess of 80 percent compared to seeding on freshly prepared seedbeds (Cross 1983). Therefore, there is a much higher probability that aerial seeding will be successful if it is conducted on a freshly disked seedbed and prior to the period when rainfall is most probable (fig. 8). Other considerations are covered by Dewald and Wiedemann (1985).

Vegetation Dynamics. Field plantings (15 x 1.5-m plots) of hulled seed (caryopsis only) and chaffy seed of WW Spar were planted in three soil types using three seeding methods and five seeding rates (Cross and Wiedemann 1985). A complete randomized block design with three replications was used. Success was judged by densities of established seedlings. In all soil types, hulled Spar plant densities were significantly greater than chaffy Spar (P<0.05). In clay loam soil, hulled Spar averaged 20.1 plants/m^2, chaffy Spar averaged 13.8 and successful stands (>5 plants/m^2) were obtained in all seeding rates (0.28, 0.56, 1.12, 2.24 and 4.48 kg PLS/ha) for both hulled and chaffy Spar. In deep fine sand, hulled Spar densities were 68% greater than those of chaffy seed. Successful stand densities were achieved at seeding rates of 0.28 and 0.56 kg PLS/ha for hulled and chaffy Spar, respectively. In loamy fine sand, successful stands did not develop due to lack of rainfall.

Table 2. Aerial seeding of field plots using a positive metering device to dispense hulled WW Spar bluestem seed mixed with cottonseed meal, or naturally slick kleingrass.

| Seeding rate | Area | Actual rates [1] | | Seeder[2] |
		Bulk	PLS	
kg PLS/ha	h	kg/ha	kg/ha	rpm
Hulled bluestem				
1/2	1.9	1.84	0.73	1050
1/2	1.9	1.75	0.68	1050[3]
1/2	3.7	1.54	0.61	850
1/2	1.9	1.55	0.62	850
1/2	3.7	1.63	0.64	850
1/2	1.9	1.55	0.62	850
1	1.9	3.87	1.53	2100[4]
1	3.7	3.00	1.19	1675
1	1.9	3.26	1.28	1675
1	1.9	2.87	1.13	1675
1	1.9	2.79	1.10	1675
1	3.7	2.63	1.03	1675
Kleingrass				
1	4.4	1.44	1.22	580
1	23.0	1.40	1.18	560

[1] Hulled Spar ≡ 78.7% PLS in cottonseed meal at 1:1 bulk w/w ratio gave 39.4% PLS mix. Kleingrass ≡ 84.1% PLS.

[2] Motor rpm registered on tachometer (not rotor speed).

[3] Seeding rate off 20%, rotor speed was adjusted by 20%.

[4] Seeding rate off 28%, rotor speed was adjusted by 20%.

Figure 8. Successful stand of aerially seeded kleingrass on rootplowed rangeland disk-chained for seedbed preparation.

CONCLUSION

The development of a disk-chain for seedbed preparation on log-littered rangeland offers a cost effective method of disturbing soil for grass seeding. Pulling the disk-chain in a triangular configuration by a single tractor provided a more practical and efficient system than the diagonal technique which required two tractors. Pulling requirements and depth of operation can be predicted over a broad range of conditions.

Improved seed metering systems for ground seeders allows the uniform dispensing of chaffy grass seed. Separate seedboxes for slick seed and chaffy seed permit a variety of grass seed mixtures to be metered accurately. Ground seeders with furrow openers gave the best results because they can overcome many of the inadequacies of seedbeds compared to the critical timing of aerial seeding for proper seedbed conditions. Ground seeders are best suited to limited acreages of land with minor amounts of brush debris.

Dispensing of aerodynamically modified chaffy seed through positive metering systems in aircraft is one of the most promising engineering advancements in the grass seeding industry. This optimism is based on the assumption that caryopses obtained by modifying chaffy grass seed may be planted without serious effects on germination and emergence. Because of the nature of grass seed, every seed lot is slightly different and meters differently. The ability to calibrate an airplane on the ground in a few minutes and then dispense load after load with little variation will be a welcome change for the commercial aerial applicator.

These recent innovative engineering developments offer pragmatic techniques to seed rangelands.

LITERATURE CITED

Bouse, L.F., J.B. Carlton and J.C. Brusse. 1982.
Dry metering system for aircraft. Trans. of the
ASAE 25(2):316-320.

Brock, J.H., E.D. Robison, C.E. Fisher and C.H.
Meadors. 1970. Reestablishment of grasses
following mechanical removal of brush. PR-
2810:43 in Brush Research in Texas 1970. Tex.
Agr. Exp. Stn. Consol. PR 2801-2828. 102 p.

Cross, B.T. 1983. Seedbeds and seeding methods.
Page 20 in H.T. Wiedemann and J.F. Cadenhead,
eds., Symposium Proc. — Range and Pasture
Seeding in the Southern Great Plains. Tex. A&M
Univ. Agri. Res. and Ext. Ctr., Vernon, TX
76384. 116 p.

Cross, B.T., and H.T. Wiedemann. 1985. Effects
of chaffy and hulled seed in the establishment
of WW Spar bluestem. Abs. of the 38th Ann.
Meet., Soc. for Range Manag. No. 281.

Dewald, C.L., A.E. Beisel and S. Cowles. 1983.
The Woodward chaffy seed conditioning system.
Pages 69-80 in H.T. Wiedemann and J.F.
Cadenhead, eds., Symposium Proc. — Range and
Pasture Seeding in the Southern Great Plains.
Tex. A&M Univ. Agr. Res. and Ext. Ctr., Vernon,
TX 76384. 116 p.

Dewald, C.L., and H.T. Wiedemann. 1985.
Improving Rangeland Seeding Success. Proc. of
the 1985 International Ranchers Roundup. Tex.
A&M Univ. Agr. Res. and Ext. Ctr., Uvalde, TX
78801.

Fisher, C.E., H.T. Wiedemann, C.H. Meadors and
J.H. Brock. 1973. Mechanical control of
mesquite. Chap. 6 in C.J. Scifres, ed.,
Mesquite. Tex. Agr. Exp. Stn. Res. Mono. 1:46-
52.

Gould, F.W. 1975. Texas Plants. Tex. Agr. Exp.
Stn., MP-585/Revised. 121 p.

Hardcastle, Harold J. 1983. Experiences in
commercial aerial seeding. Page 44-45 in H.T.
Wiedemann and J.F. Cadenhead, eds., Symposium
Proc. — Range and Pasture Seeding in the
Southern Great Plains. Tex. A&M Univ. Agr. Res.
and Ext. Ctr., Vernon, TX 76384. 116 p.

Wiedemann, H.T. 1982. Fluffy grass seed metering
device for rangeland seeders. Pages 178-182 in
E.F. Aldon and W.R. Oaks, eds., Symposium Proc.
- Reclamation of Mined Land in the Southwest.
Soil Cons. Soc. of Amer., Box 2142, Albuquerque,
NM 87102. 218 p.

Wiedemann, H.T. 1984. Fluffy seed metering
systems for drills. Pages 36-42 in H.T.
Wiedemann and J.F. Cadenhead, eds., Symposium
Proc. — Range and Pasture Seeding in the
Southern Great Plains. Tex. A&M Univ. Agr. Res.
and Ext. Ctr., Vernon, TX 76384. 116 p.

Wiedemann, H.T. 1985. To restore rangelands ...,
Agr. Eng. 66(11):8-10.

Wiedemann, H.T., and J.H. Brock. 1975. Reseeding
as affected by seedbed preparation, seeding
methods and seeding rates following rootplowing.
Pages 38-40 in Rangeland Resources Research
1971-74. Tex. Agr. Exp. Stn. Consol. PR 3341.
70 p.

Wiedemann, H.T., and B.T. Cross. 1982. Draft of
disk-chains for rangeland seedbed preparation.
Trans. of the ASAE 25(1):74-76,80.

Wiedemann, H.T., and B.T. Cross. 1983.
Microprocessor with memory chip to collect
transducer data on mobile equipment. Agr. Eng.
64(11):7-8, 11.

Wiedemann, H.T., and B.T. Cross. 1985a.
Influence of operating mass on disk-chain
performance. ASAE paper No. 85-1612. ASAE, St.
Joseph, MI 49085.

Wiedemann, H.T., and B.T. Cross. 1985b.
Influence of pulling configuration on draft of
disk-chains. Trans. of the ASAE 28(1):79-82.

Wiedemann, H.T., C.H. Meadors and B.T. Cross.
1980. Hopper-gate baffel for improved aerial
metering of pelleted herbicides and seed. Pages
98-99 in Rangeland Resource Research. Tex. Agr.
Exp. Stn. Consol. PR 3665.

Wiedemann, H.T., J.H. Brock, C.E. Fisher and B.T.
Cross. 1979. Seed metering and placement
devices for rangeland seeder. Trans. of the
ASAE 22(5):972-977.

USDA Forest Service. 1986. Develop and test disk-
chain implement--final report. Missoula Equip-
ment Development Center. Missoula, MT 59801.

ESTABLISHING GRASSES BY IMPRINTING IN THE
NORTHWESTERN UNITED STATES

M.R. Haferkamp[1], D.C. Ganskopp[1], R.F. Miller[2],
F.A. Sneva[3], K.L. Marietta[4] and D. Couche[5]

ABSTRACT

Broadcasting seed and land imprinting was
compared with broadcasting and chaining and
drilling for establishing crested wheatgrass
[Agropyron desertorum (Fisch. ex Link)] and
bluebunch wheatgrass [Agropyron spicatum[6] (Pursh)
Scribn. and Smith] in the northern Great Basin
and Palouse Prairie. Land imprinting was most
effective on loose or coarse textured soils.

INTRODUCTION

Drilling has conventionally been used to seed
rangelands in the western United States.
Planting with a drill provides uniform distribu-
tion of seed and proper depth of planting on firm
seedbeds. On loose soils packing is usually
required to achieve the degree of soil firmness
needed for optimum control of planting depth,
improved water holding capacity of the surface
soil, enhanced capillary transfer of water to the
seed, and optimum seed to soil contact (Hyder et
al. 1955, Hyder and Sneva 1956, McGinnies 1962,
Hyder and Bement 1969, Hyder and Bement 1970).

Broadcasting is employed where topography is too
rough for drills to be used or where vast areas
must be seeded, such as following large fires.
Broadcast seeds are exposed to rapidly fluctuat-
ing moisture and temperature extremes and
depredation by birds and rodents. Thus seed

[1]Range Scientist, USDA-ARS, Eastern Oregon
Agricultural Research Center, Squaw Butte
Station, Star Rt. 1, 4.51 Hwy. 205, Burns, Oregon
97720.

[2]Associate Professor, Oregon State Univer-
sity, Eastern Oregon Agricultural Research
Center, Squaw Butte Station, Star Rt. 1, 4.51
Hwy. 205, Burns, Oregon 97720.

[3]Range Scientist (retired), USDA-ARS,
Eastern Oregon Agricultural Research Center,
Squaw Butte Station, Star Rt. 1, 4.51 Hwy. 205,
Burns, Oregon 97720.

[4]Research Assistant, Oregon State Univer-
sity, Eastern Oregon Agricultural Research
Center, Squaw Butte Station, Star Rt. 1, 4.51
Hwy. 205, Burns, Oregon 97720.

[5]Range Conservationist, USDA-SCS, P.O. Box
195, Enterprise, Oregon 97828.

[6]Pseudoroegneria spicata (Pursh) A. Love
has been proposed to replace the name Agropyron
spicatum (Pursh) Scribn. and Smith (Barkworth et
al. 1983)

should be covered with soil when possible (Nelson
et al. 1970, Goebel 1978). Chaining and other
methods have been used to cover broadcast seeds
(Vallentine 1980, Luke and Monsen 1984).

The land imprinter (Dixon and Simanton 1980,
Anderson 1981) and the imprinting revegetation
system (Dixon 1982) appear to be effective for
covering broadcast seed and for creating microde-
pressions to reduce runoff. Results from imprint-
ing have been variable in the southwestern United
States, where much of the precipitation occurs as
intense summer rains (Dixon 1980, Tye 1980, Dixon
1983, Dale 1985, Cox et al. 1986). In that
environment, retention of water is critical to
provide adequate moisture for seed germination and
seedling establishment.

Prior to 1982, data comparing the imprinter to
other commonly used equipment were lacking in the
northwestern United States. One exception was a
study initiated following a wildfire in Utah in
October 1981 to compare the effectiveness of
broadcasting seed and imprinting to drilling
(Clary and Johnson 1983, Clary and Wagstaff 1987).
To fill this information void a series of studies
was initiated to compare effectiveness of broad-
casting seed and land imprinting with broadcasting
before chaining and drilling for fall planting
cool-season grasses on a variety of seedbeds in
the Palouse Prairie and northern Great Basin.

METHODS

Palouse Prairie

A study was initiated in 1982 to evaluate reestab-
lishment of weeds and establishment of Nordan
crested wheatgrass and Secar bluebunch wheatgrass
following seedbed preparation on ash covered
rangelands in the Palouse Prairie (Haferkamp et
al. 1985). The study site located 43 km east of
Ritzville, Washington, is representative of areas
receiving a 5-cm deposition of ash of silt loam
texture from the Mount St. Helens eruption
occurring in 1980. Soils are in the Benge series,
silt loam in texture, and occur on 0-15% slopes.
Elevation is 560 m, and over 50% of the annual
31 cm of precipitation occurs during November
through February. Vegetation consists mainly of
annual grasses, forbs and bluegrasses (Poa spp.)
with scattered plants of bluebunch wheatgrass and
Thurber needlegrass (Stipa thurberiana Piper).
Dominant annual grasses include downy brome
(Bromus tectorum L.) and Ventenata dubia (Leers)
Coss.& Dur.

Seedbeds were prepared by several techniques
listed in Table 1. Crested wheatgrass seed was
planted at 6.7 kg pure live seed (PLS)/ha with a
rangeland drill equipped with single-disk openers
and 25-mm depth bands or broadcast after plots
were rolled with a water-filled land imprinter
(2 m wide, 1-m diameter, 10-cm pattern depth,
4.1-Mg weight). Bluebunch wheatgrass seed was
planted at 7.0 kg PLS/ha with the rangeland drill
or by broadcasting before or after plots were
rolled with the imprinter. All plantings were
made in October 1982.

Table 1. Seedbed preparation techniques applied
on experimental range seeding plots in
1981 and 1982 east of Ritzville,
Washington.

Undisturbed-Control

Herbicide
  Spring applied
    Glyphosate-1.12 kg/ha
    Paraquat-0.56 kg/ha
  12-month fallow
    Atrazine-0.56 kg/ha

Disking
  Spring
  Fall

Burning
  Summer
  Fall

Summer Burning + Fall Applied Herbicide
  Glyphosate-1.12 kg/ha
  Paraquat-0.56 kg/ha

Treatments were replicated three times and
arranged in a strip-plot design with seedbed
preparation as main plots and planting method-
species combinations as subplots. Each subplot
measured 9 by 18 m. Success of treatments was
evaluated by determining density of competing
species in early May 1983 in 10, 15- by 15-cm
quadrats per subplot and measuring frequency and
density of crested and bluebunch wheatgrass
seedlings in mid-June 1983 and plants in mid-June
1984 in 10, 30- by 60-cm quadrats per subplot.
Analysis of variance was used to test the effect
of seedbed preparation method and species-
planting technique combinations. Mean separation
tests were made using $LSD_{0.05}$.

Squaw Butte

A study was initiated in 1982 on a Wyoming big
sagebrush (Artemisia tridentata wyomingensis
Beetle)-Thurber needlegrass habitat type located
on the Squaw Butte Experiment Station, 68 km west
of Burns, Oregon (Haferkamp et al. 1987).
Elevation is 1,372 m and the soils are mainly
Gradon Variant gravelly fine sandy loams (fine-
loamy, mixed, frigid Orthidic Durixerolls) and
some Ratto gravelly fine sandy loams (clayey,
montmorillonitic, frigid, shallow Xerollic
Durargids). The dominant shrubs, Wyoming big
sagebrush and green rabbitbrush [Chrysothamnus
viscidiflorus (Hook.) Nutt.], provide about 15%
canopy cover (Doescher et al. 1984). Dominant
grasses, squirreltail [Sitanion hystrix
(Nutt.)J.G.Sm.], Sandberg bluegrass (Poa
sandbergii Vasey), and Thurber needlegrass,
provide 21.3% basal cover. Peak standing herbage
production was 627 kg/ha in 1982, a wet year.
Mean annual precipitation is 29 cm with peak
accumulation occurring in the October to June
period.

Seedbeds were either unprepared or prepared by
mowing with a rotobeater (Vallentine 1980) or
mowing plus disking. Mowing killed mature
sagebrush plants and left a firm seedbed with live
herbaceous and green rabbitbrush plants. Mowing
plus disking killed most shrubs and herbaceous
plants and provided a loose seedbed. Plot
preparation in 1982 and 1984 included mowing and
disking in August to destroy established plants,
redisking in September after fall rains to destroy
downy brome seedlings, and planting in October.
Preparation by disking in 1984 followed a similar
schedule but utilized plots that had been mowed in
1982. Soil water content at planting in the 0- to
5-cm depth on unprepared, brushbeat and brushbeat-
disked seedbeds averaged 8.2, 9.9, and 8.1% of
oven-dried weight in 1982; and 4.8, 4.2, and 6.2%
in 1984, respectively. Soil water content at
-1.5 MPa averaged 9.0%

Seeding methods included broadcasting in front of
a water-filled imprinter, broadcasting after
imprinting, drilling with a rangeland drill
equipped with single-disk openers on 30-cm centers
with 25-mm depth bands, and drilling with a
rangeland drill equipped with deep-furrow openers
on 60-cm centers. Nordan crested wheatgrass seed
was planted at 6.7 kg PLS/ha in each plot planted
by broadcasting or drilling with regular openers
and 3.4 kg PLS/ha in plots planted by drilling
with-deep furrow openers.

Four replications were arranged in a strip-plot
design with years as main plots, seedbed prepara-
tion as subplots, and planting methods as sub-
subplots. Each sub-subplot measured 15 by 30 m.
Density and frequency of crested wheatgrass
seedlings or plants were determined in 10, 30- by
60-cm quadrats per sub-subplot in September 1983
and August 1984 in the 1982 planting and in July
1985 and July 1986 in the 1984 planting. Canopy
cover of shrubs and basal cover of other grasses
were determined on both seedings by line intercept
in 1985. Analysis of variance was used to test
effect of years, methods of seedbed preparation,
methods of planting and interactions. Mean
separation tests were made using $LSD_{0.05}$.

Alkali Lake

A study was begun in 1983 following a wildfire in
July, which removed most vegetative cover from a
large area just south of Alkali Lake, Oregon
(Ganskopp 1985). The soil is an Olson fine sandy
loam (loamy mixed frigid shallow Xerollic Durar-
gids). Wyoming big sagebrush and spiny hopsage
[Grayia spinosa (Hook.) Moq.] dominate the
overstory, with Indian ricegrass [Oryzopsis
hymenoides (R.& S.) Ricker] and squirreltail as
understory dominants. The annual precipitation is
similar to Squaw Butte, with peak periods in fall,
winter, and spring.

A helicopter broadcast a mixture of cereal rye
(Secale cereale L.) at 15.7 kg/ha and Nordan
crested wheatgrass at 7.8 kg/ha on the burned
seedbed in October 1983. After broadcasting seed,

three treatments were applied to the seedbed. These included: 1. Chaining, with a large anchor chain (22.7 to 31.8-kg links) stretched between two crawler tractors and pulled over the seedbed; 2. Imprinting with a land imprinter weighing 4.1 Mg; and 3. Untreated. Three replications were arranged in a randomized complete-block design. Each plot measured 50 by 100 m.

Success of treatments was evaluated in midsummer 1984 and 1985 by determining density of cereal rye, crested wheatgrass, and downy brome plants in 25, 30- by 60-cm quadrats per plot. Data were analyzed by analysis of variance and means were separated by $LSD_{0.05}$.

Fossil Beds and Diamond

Two studies were planted in fall 1985 to determine the effect of seeding rate on seedling and plant density for Nordan crested wheatgrass, Secar bluebunch wheatgrass, and T-2950 bluebunch wheatgrass. Plots were planted by broadcasting in front of a land imprinter or with a rangeland drill.

The Fossil Beds study site, a deteriorated Wyoming big sagebrush-bluebunch wheatgrass community, is located 11 km northwest of Dayville, Oregon. Soil is a Simas clay loam. Vegetation on the site prior to the study consisted of annual grasses and forbs including: downy brome, bur buttercup (Ranunculus testiculatus Crantz), wallflower mustard (Erysimum repandum L.), Jim Hill tumble mustard (Sisymbrium altissimum L.), and blue mustard [Chorispora tenella (Pall.) DC].

The seedbed was disked in April and again in June 1985. Secar bluebunch wheatgrass and T-2950, an experimental cultivar of bluebunch wheatgrass, obtained from the USDA Soil Conservation Service plant materials center, Aberdeen, Idaho, were planted in November 1985 by broadcasting seed on disked seedbeds and then rolling plots with an imprinter weighing 2.6 Mg. Secar was planted at 215, 430, and 645 PLS/m² (6.0, 11.9, and 17.9 kg PLS/ha), and T-2950 was planted at 215 PLS/m² (9.7 kg PLS/ha). Four replications were arranged in a randomized complete-block design. Each plot measured 17 by 22 m.

Bluebunch wheatgrass seedling density and frequency were determined in 10, 30- by 60-cm quadrats per main plot in early April 1986 and March 1987, weed seedling density was determined in 10, 30- by 60-cm quadrats per replication in late April 1986, and canopy cover of competing species was determined in May and June 1986. Weed standing crops were sampled in June 1986. Samples were harvested to ground level by clipping and oven-dried at 60°C for 24 hours before weighing. Data were analyzed by analysis of variance and means were separated by $LSD_{0.05}$.

An abandoned field located about 11.3 km northeast of Diamond, Oregon, was disked in May 1985, cultivated with a spike-tooth harrow (Vallentine

1980) in October 1985 to kill downy brome seedlings that had emerged following fall rains and planted in October 1985. The soil is an unclassified loam, and the annual precipitation averages 29.0 cm. Nordan crested wheatgrass was planted with a rangeland drill at 344 PLS/m² (9.5 kg PLS/ha) and broadcast in front of an imprinter at 172, 258, or 344 PLS/m² (4.7, 7.1, and 9.5 kg PLS/ha). The drill was equipped with single disk openers with depth bands, and the imprinter weighed 2.6 Mg. In an adjacent study, T-2950 bluebunch wheatgrass seed was broadcast in front of an imprinter at 215, 323, or 430 PLS/m² (8.8, 13.2, and 17.6 kg PLS/ha). In each study, four replications were arranged in a randomized complete block design. Each plot measured 20 by 30 m. Density of crested and bluebunch wheatgrass seedlings and plants were determined in 10, 15- by 30-cm quadrats per plot in mid-May 1986 and in late March 1987. In the Nordan study, data were analyzed by analysis of variance and means separated by $LSD_{0.05}$. T-2950 data were analyzed by regression analysis.

RESULTS AND DISCUSSION

Vallentine (1980) reported that on seeded foothill range in the Intermountain Region in the 28- to 33-cm precipitation zone, stands were evaluated based on the density of seeded plants. Stands were excellent when plant densities were greater than 8.0/m² and good if plant densities were between 5.5 and 8.0/m². These will be used as standards of comparisons in discussing the current studies.

Palouse Prairie

Precipitation for weather stations in the Palouse Prairie east of Ritzville, Washington, totaled 37 cm for October 1982 through June 1983 and 43 cm for July 1983 through June 1984. During both years precipitation was above average.

Burning seedbeds removed the dense layer of litter that was present on undisturbed seedbeds, while disking incorporated litter into the soil. Compared to control plots, density of annual forbs was significantly decreased by Atrazine fallow, fall disking, burning and summer burning + fall spraying (Table 2). Density of downy brome seedlings was significantly decreased by summer burning alone and summer burning combined with spraying. Summer burning was conducted when the majority of downy brome seeds were still held in the inflorescences, and fall spraying was conducted after downy brome seedlings had emerged. Density of other annual grasses, predominantly V. dubia, was increased significantly compared to control plots by most treatments except fall disking and burning. Past research has shown plantings of perennial forage species on downy brome ranges have often resulted in failures, mainly because of competition between seedlings and downy brome plants during the first growing season (Klomp and Hull 1972). Less is known about V. dubia, but phenologically it develops later

Table 2. Density of competing herbaceous species in 1983 on experimental seeding plots located east of Ritzville, Washington after seedbed preparation in 1981 and 1982.

Species	Control	Herbicide			Disk		Burn		Summer Burn	
		Gly.	Par.	Atr.	Spr.	Fall	Sum.	Fall	Gly.	Par.
					seedlings/m^2					
Annual forbs	879	959	787	611	757	441	603	464	403	583
Annual grasses	166	547	948	1224	611	271	602	296	527	509
Downy brome	240	172	255	321	255	202	90	205	37	36
Total	1285	1678	1990	2156	1623	914	1295	965	967	1128

$LSD_{0.05}$ = 237, for annual forbs.
$LSD_{0.05}$ = 359, for annual grasses.
$LSD_{0.05}$ = 126, for downy brome.

than downy brome, and thus may not compete as severely with emerging seedlings.

Emergence of Nordan seedlings was good the first summer after fall planting on a variety of seedbeds planted by drilling or broadcasting seed onto imprinted seedbeds (Table 3). Successful establishment of plants, however, occurred only from drilling on the burned and summer-burned + fall-sprayed seedbeds and from imprinting on the summer-burned + fall-sprayed seedbeds. Establishment from drilling on burned seedbeds was significantly better than on control, herbicide treated, or disked seedbeds, and when fall spraying was combined with summer burning, establishment was significantly increased over burning alone. Imprinting on summer-burned + Glyphosate-sprayed seedbeds resulted in significantly better establishment from broadcasting seed than occurred on other seedbeds. Establishment on summer-burned + Paraquat-sprayed seedbeds was significantly better than establishment on all but summer-disked seedbeds. Drilling resulted in significantly better establishment than imprinting on fall-burned and summer-burned + fall-sprayed seedbeds.

Table 3. Nordan crested wheatgrass seedling and plant density in 1983 and 1984 on experimental plots planted in fall 1982 east of Ritzville, Washington.

Year and Planting Method	Control	Herbicide			Disk		Burn		Summer Burn	
		Gly.	Par.	Atr.	Spr.	Fall	Sum.	Fall	Gly.	Par.
					seedlings/m^2					
1983										
Drill	1	5	8	3	7	7	19	22	41	46
Imprint	T[1]	1	1	1	5	12	17	3	23	20
					plants/m^2					
1984										
Drill	1	0	0	0	1	0	6	5	16	17
Imprint	0	0	1	0	1	2	3	1	10	5

$LSD_{0.05}$ = 12, between planting methods on same seedbed, 1983.
$LSD_{0.05}$ = 11, between seedbeds with same planting method, 1983.
$LSD_{0.05}$ = 4, between planting methods on same seedbed, 1984.
$LSD_{0.05}$ = 3, between seedbeds with same planting method, 1984.
[1]T Less than 0.5

Secar seedling emergence and plant establishment followed a trend similar to Nordan with good emergence occurring on a variety of seedbeds planted by drilling or broadcasting and imprinting (Table 4). Successful establishment occurred with drilling on burned and summer-burned + fall-sprayed seedbeds. Imprinting resulted in establishment approaching good on fall-disked and summer-burned + Paraquat-sprayed seedbeds, but overall results were too variable to clearly determine the best seedbed-planting method

combination for imprinting. Whether seeds were broadcast in front of the imprinter or onto imprinted seedbeds did not appear to affect success of establishment.

Plant densities usually decreased the second summer compared to seedling densities the first summer. This decrease in density was due in part to seedling mortality and the fact clustered seedlings counted as individuals in year one could not be identified as individuals in year two.

Drilled Nordan was more evenly distributed on fall-burned and summer-burned + fall- sprayed seedbeds and on disked seedbeds (Table 5). Frequency on imprinted seedbeds ranged from 40 to 73% with burning and burning + spraying and 47 to 77% with disking. Plants were less frequent the second summer. Nordan frequencies averaged 53 to 77% on fall-burned and burned + sprayed seedbeds planted by drilling and 50 to 70% on burned + sprayed seedbeds planted by imprinting. All other Nordan frequencies were less than 30%. Frequency of distribution of Secar seedlings and plants followed similar trends.

Table 4. Secar bluebunch wheatgrass seedling and plant density in 1983 and 1984 on experimental plots planted in fall 1982 east of Ritzville, Washington.

Year and Planting Method	Control	Seedbed Preparation Method								
		Herbicide			Disk		Burn		Summer Burn	
		Gly.	Par.	Atr.	Spr.	Fall	Sum.	Fall	Gly.	Par.
		- - - - - - - - - - - - - seedlings/m^2 - - - - - - - - - - - - -								
1983										
Drill	2	6	6	2	8	4	30	28	37	44
Seed imprint	0	2	1	T[1]	4	13	9	5	12	8
Imprint seed	0	1	3	1	7	13	6	9	16	15
		- - - - - - - - - - - plants/m^2 - - - - - - - - - - - - -								
1984										
Drill	0	0	T	0	T	1	7	6	10	14
Seed imprint	0	T	0	0	T	3	1	1	2	5
Imprint seed	T	T	0	T	T	5	1	1	4	3

$LSD_{0.05}$ = 12, between planting methods on same seedbed - 1983.
$LSD_{0.05}$ = 11, between seedbeds with same planting method - 1983.
$LSD_{0.05}$ = 4, between planting methods on same seedbed - 1984.
$LSD_{0.05}$ = 3, between seedbeds with same planting method - 1984.

Table 5. Frequency of distribution of Nordan crested wheatgrass and Secar bluebunch wheatgrass seedlings in July 1983 on experimental plots planted in October 1982 east of Ritzville, Washington.

Species and Planting Method	Control	Seedbed Preparation Method								
		Herbicide			Disk		Burn		Summer Burn	
		Gly.	Par.	Atr.	Spr.	Fall	Sum.	Fall	Gly.	Par.
		- - - - - - - - - - - - - - - - - % - - - - - - - - - - - - - - - - -								
Nordan										
Drill	13	50	70	43	60	53	67	90	100	97
Imprint	7	17	17	17	47	77	60	40	73	63
		- - - - - - - - - - - - - - - - - % - - - - - - - - - - - - - - - - -								
Secar										
Drill	20	43	40	37	53	43	83	87	100	100
Seed Imprint	0	23	13	7	37	53	57	50	77	60
Imprint Seed	0	17	20	17	60	77	37	73	90	83

These results demonstrate the well known positive relationship between successful plant establishment and planting seed into mineral soil on seedbeds where downy brome seedling density has been reduced. These conditions were met on the summer-burned and summer-burned + fall-sprayed seedbeds, where mineral soil was exposed by burning and downy brome seedling density was

reduced to less than 90 seedlings/m^2 with summer burning and to less than 40/m^2 with burning combined with fall spraying.

The best explanation for increased establishment from drilling compared to broadcasting and imprinting on what appears to be the best prepared seedbed, summer-burned + fall-sprayed, is that

drilling resulted in better seed distribution and seed to soil contact. When seed was planted by drilling on the firm-burned seedbed, planting depth was controlled by depth bands, and essentially all of the seed was planted into the furrows formed by the disk openers and covered with loose soil by pipes pulled behind each opener. In contrast, the water-filled imprinter was not heavy enough to allow full penetration and formation of 10-cm deep imprints. Instead only shallow grooves were formed by the outer edges of the angle iron welded to the outside of the metal cylinder. Thus, compared to drilling relatively more broadcast seeds were left exposed on the soil surface between the shallow grooves, and we speculate seed to soil contact was not optimum except possibly in grooves where seed was broadcast in front of the imprinter.

Squaw Butte

Fall precipitation was similar (8.6 and 8.0 cm) for the 2 planting years, but precipitation during winter, spring, and summer was 8.9, 10.8 and 4.9 cm in 1982-83 and 2.8, 5.5 and 2.0 cm in 1984-85. Basal cover of native grasses was significantly reduced from an average of 3.0% on unprepared and mowed seedbeds to less than 1.0% by disking after mowing. Canopy cover of shrubs was reduced from 13.0% on unprepared seedbeds to 4.0% with mowing and disking.

Significantly more seedlings emerged on mowed-disked compared to unprepared and mowed seedbeds planted by drilling with regular openers and broadcasting seed before or after imprinting (Table 6). On unprepared and mowed seedbeds, seedlings were more dense when seeds were planted by drilling with regular openers, but emergence on a per row basis was similar, $10/m^2$, for the two drilling treatments since drilling with

regular openers planted twice as many rows per plot as deep-furrow drilling (Table 6). Excellent stands of seedlings emerged on mowed-disked seedbeds planted by broadcasting seed in front of the imprinter. Broadcasting seed in front of the imprinter on this loose seedbed increased seedling emergence two and three times more than drilling with regular openers or broadcasting seeds onto the imprinted seedbed.

Averaged across years, significantly more plants were established by drilling with regular openers on mowed-disked compared to unprepared and mowed seedbeds (Table 6). As with seedling densities, plant densities/m^2 were greatest when seeds were planted by drilling with regular openers on unprepared and mowed seedbeds. In contrast to the first summer, plant densities were similar on mowed-disked seedbeds planted by broadcasting seed before imprinting and drilling with regular openers. Significantly more plants were established by these two techniques than by broadcasting after imprinting or deep-furrow drilling.

Seedlings were most evenly distributed on seedbeds prepared by mowing and disking and planted by regular drilling (88%) and broadcasting with imprinting (79-91%). Seedling distribution was intermediate on unprepared or mowed seedbeds planted by drilling (45-53%). Poorest seedling distribution occurred on unprepared and mowed seedbeds planted by imprinting (21-36%) and brushbeat-disked seedbeds planted by deep-furrow drilling (25%). Plant distribution the second summer was similar to seedling distribution the first summer. In general, plants were more evenly distributed in the 1982 seeding than the 1984 seeding, probably a result of more precipitation and better growing conditions in 1983 compared to 1985.

Table 6. Nordan crested wheatgrass seedling density the first summer after planting and plant density the second summer after planting on experimental range seeding plots planted in 1982 and 1984 on the Squaw Butte Experimental Range. Data are averaged across planting years.

Seedbed Preparation Method	Planting method			
	Regular Drill	Deep-furrow[1] Drill	Seed Imprint	Imprint Seed
	-------------------------seedlings/m^2-------------------------			
Unprepared	7	3	3	2
Mowed	8	5	3	1
Mowed-disked	16	1	30	10
	-------------------------plants/m^2-------------------------			
Unprepared	9	4	4	4
Mowed	9	5	5	4
Mowed-disked	19	2	18	11

$LSD_{0.05}=7$, between seedbeds with same planting method
$LSD_{0.05}=6$, between planting methods on same seedbed
$LSD_{0.05}=5$, between seedbeds with same planting method
$LSD_{0.05}=6$, between planting methods on same seedbed

The increase in seedling density with imprinting probably resulted from packing loose soil, improving seed to soil contact and planting more crested wheatgrass seeds at the proper depth. This supposition is supported by emergence of fewer seedlings on mowed-disked plots planted by drilling with regular openers and broadcasting seed after imprinting. More seedlings were also observed on ridges formed by the imprinter when seed was broadcast in front of the imprinter than when seed was broadcast onto the imprinted soil surface.

Reduced seedling emergence with imprinting compared to drilling on relatively firm seedbeds (no preparation and mowing) was due to poor penetration by the imprinter. On these seedbeds the imprinter was not heavy enough to form complete imprints. In contrast, furrow openers effectively removed competition in strips, and seed was planted into a firm seedbed and covered with loose soil. The requirement for reduction of competition for successful establishment of crested wheatgrass stands was obvious. Density of emerging seedlings was increased whether the reduction of competition resulted from furrow openers or disking.

Alkali Lake

High winds occurred on these plots, 5 days after seedbed treatments were applied, and blowing soil eliminated all visual evidence of imprinting or chaining. Precipitation from November 1983 through July 1984 totaled 23.4 cm, providing slightly less than normal moisture for developing seedlings. Seedling and plant densities of cereal rye and crested wheatgrass were about four times greater on imprinted areas than on chained and untreated areas in 1984 (Table 7). However, all stands were considered excellent.

Densities of cereal rye tended to decrease over time and by 1985 and 1986 were similar on all seedbeds. Crested wheatgrass plants were about three times more dense on imprinted areas than on untreated and chained areas in 1985 and 1986. Density of downy brome plants declined in 1986 on imprinted areas supporting the densest stands of crested wheatgrass.

In this study timing, soils, and precipitation patterns probably were ideal for broadcast seeding since seeding was accomplished just before fall rains. The improved emergence from the imprint treatment was probably related to compaction of the loose seedbed and retention of this compaction even though imprint depressions and seed were covered by blowing soil. The importance of compaction was also evident on chained areas where seedling emergence was most prevalent where tractor tracks compacted and indented the loose mineral soil. Clary (personal communication) also reported good seedling emergence on imprinted plots following wind erosion in Utah.

Fossil Beds and Diamond

Precipitation during the Fossil Beds study totaled 22.0 cm for September through May 1985-86 and 15.0 cm for September through March 1986-87. Seedling density of bluebunch wheatgrass growing near Dayville, Oregon, determined in April when seedlings were in the 2- to 5-leaf stage, was excellent for all treatments (Table 8). Increasing the seeding rate from 200 PLS/m^2 to 600 PLS/m^2 significantly increased seedling density of Secar bluebunch wheatgrass, but this increased density may or may not be beneficial to the subsequent stand. Plant distribution was good (90 to 100% frequency) in all plots. These stands developed with weedy competition from bur buttercup, Jim Hill mustard, blue mustard, and downy brome.

Table 7. Seeding and plant density of cereal rye, crested wheatgrass and downy brome growing on experimental range seeding plots planted in October 1983 near Alkali Lake in Oregon.

| Species | Year | Seedbed Preparation Method | | | LSD$_{0.05}$ |
		Unprepared	Chained	Imprinted	
		- - - - - - - - number/m^2 - - - - - - - -			
Cereal Rye	1984	3	4	17	6
	1985	3	4	6	_[1]
	1986	1	1	1	-
Crested Wheatgrass	1984	8	9	48	35
	1985	10	13	39	21
	1986	9	12	33	5
Downy Brome	1984	6	4	4	-
	1985	41	20	21	-
	1986	21	20	4	-

[1]Means are not significantly different.

Density of competing species was 115/m^2 in April and by June canopy cover was estimated at 86% and standing crop averaged 5170 kg/ha. Plant densities were excellent for all treatments in March 1987. Although plant density increased with increases in seeding rate, the lowest seeding rate appears adequate for both Secar and T-2950.

Seedling emergence of Nordan crested wheatgrass at Diamond was excellent for all seeding rates and planting methods (Table 9). Significantly more seedlings emerged on plots broadcast with 344 PLS/m^2 and then imprinted compared to other treatments. By March 1987, densities of established plants averaged 27/m^2, but densities were similar between treatments. An average of 25, 42, and 41, T-2950 seedlings/m^2 emerged from seeding rates of 215, 323, and 430 PLS/m^2. Although more seedlings emerged from the two highest rates, the increase was not significant. By March 1987, 18, 18 and 26 plants/m^2 were established in plots planted with 215, 323 and 430 PLS/m^2. The linear relationship ($Y = 8.35 + 0.04X$) was significant ($p = 0.05$) with $r^2 = 0.34$. Seedling and plant distribution were very even with frequencies ranging from 80 to 100%.

Table 8. Density of Secar and T-2950 bluebunch wheatgrass seedlings the first summer and plants the second summer growing on experimental plots planted in fall 1985 on the John Day Fossil Beds National Monument located north of Dayville, Oregon.

Year and Accession	Seeding Rate (PLS/m^2)		
	215	430	645
	- - - - - - -seedlings/m^2 - - - - - -		
1986			
Secar	33	53	99
T-2950	51	–	–
	LSD$_{0.05}$ = 63		
	- - - - - - - plants/m^2 - - - - - - -		
1987			
Secar	20	30	47
T-2950	17	–	–
	LSD$_{0.05}$ = 6		

Table 9. Density of Nordan crested wheatgrass seedlings in May 1986 and plants in March 1987 on experimental plots planted in October 1985 west of Diamond, Oregon.

Year and Planting Method	Seeding Rate (PLS/m^2)		
	172	258	344
	- - - - - - - seedlings/m^2 - - - - - -		
1986			
Imprint	61	66	120
Drill	–	–	78
	LSD$_{0.05}$ = 40		
	- - - - - - - - -plants/m^2 - - - - - -		
1987			
Imprint	23	26	30
Drill	–	–	29

Dixon (1982) suggested seeding rates with imprinting should be 1.5 times the rate used with drilling when the land imprinter was used as the primary method of seedbed preparation and seeding. Results from prior studies at the Fossil Beds National Monument (M.R. Haferkamp, unpublished data) suggested seeding rates of Secar bluebunch wheatgrass needed to be increased to greater than 200/m^2, while preliminary results from the imprinting study at Squaw Butte suggested seeding rates for Nordan crested wheatgrass could be reduced.

Results from the current studies indicate excellent stands of Secar and T-2950 bluebunch wheatgrass and Nordan crested wheatgrass seedlings emerged on disked plots. These results suggest that good to excellent stands may be established with even lower seeding rates than evaluated. This question needs to be addressed in other

studies with variable soils and climatic conditions.

CONCLUSIONS

The land imprinter appears to be a useful implement used in combination with broadcasting seed for planting loose or coarse textured soils in the northern Great Basin. With the imprinter as with other types of roller or press wheel seeders (Beutner and Anderson 1944, Hyder et al. 1961, Hyder and Bement 1969, Hyder and Bement 1970, Marlatt and Hyder 1970, Vallentine 1980), loose soil can be firmed prior to or during planting, thus, improving seed to soil contact. Possibly even more important seeds will be planted at a more optimum depth. When working on firm soils, other techniques, i.e. drilling appear better, since full 10-cm imprints are not formed and much of the broadcast seed is left uncovered on the soil surface. The major benefits of forming full imprints are more of the seed broadcast in front of the imprinter will be pressed into the soil, improving seed to soil contact; deeper imprints provide emerging seedlings some protection from wind; and the rougher surface occurring with deeper imprints should enhance snow catchment and water infiltration compared to a smoother surface.

At one time, the land imprinter was proposed as a primary implement for seedbed preparation (Larson 1980). It is doubtful the implement can be used effectively without some prior method of seedbed preparation, designed to control competing vegetation in the northern Great Basin or the Palouse Prairie. Without control of competition, i.e. annual grasses (downy brome and V. dubia), perennial grasses (Sandberg bluegrass), or sprouting shrubs (green rabbitbrush) seedlings of seeded species may emerge in years of above average precipitation, but they may not persist, and stand productivity may be poor in future years.

ACKNOWLEDGEMENTS

LITERATURE CITED

Anderson, R. 1981. A story in two parts, advance of the barren earth, technology for reversing desertification. Rangelands 3:47-50.

Barkworth, M.E., D.R. Dewey, and R.J. Atkins. 1983. New generic concepts in the Triticeae of the Intermountain region: Key and comments. Great Basin Natural. 43:561-572.

Beutner, E.L., and D. Anderson. 1944. Notes - A method of seedbed preparation and reseeding deteriorated rangelands. J. Amer. Soc. Agron. 36:171-172.

Clary, W.C., and T.J. Johnson. 1983. Land imprinter results in Utah, p.23-24. In: 37th annual report, Vegetative rehabilitation & equipment workshop. 13-14 February 1983, Albuquerque, New Mexico. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Clary, W.C., and F.J. Wagstaff. 1987. Biological and economic effectiveness of several revegetation techniques in the pinyon-juniper-sagebrush zone, p.305-312. In: Everett. R.L. (compiler) Proceedings--pinyon-juniper conference. 13-16 January 1986, Reno, Nevada. USDA Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-215.

Cox, J.R., M.H. Martin-R., F.A. Ibarra-F., and H.L. Morton. 1986. Establishment of range grasses on various seedbeds at creosotebush (Larrea tridentata) sites in Arizona, U.S.A., and Chihuahua, Mexico. J. Range Manage. 39:540-546.

Dale, D. 1985. Homemade device "impressively" reclaims rangeland gone to brush. Beef - 22(1):58-61.

Dixon, R. 1980. Rangeland imprinter, p. 8-9. In: 34th annual report, Vegetative rehabilitation & equipment workshop. 10-11 February 1980, San Diego, California. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Dixon, R. 1982. Land imprinting activities, p. 20-21. In: 36th annual report, Vegetative rehabilitation & equipment workshop. 4-5 February 1982, Denver, Colorado. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Dixon, R. 1983. Land imprinting activities, p. 13. In: 37th annual report, Vegetative rehabilitation & equipment workshop. 13-14 February 1983, Albuquerque, New Mexico. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Dixon, R.M., and J.R. Simanton. 1980. Land imprinting for better watershed management, p. 809-826. In: Symposium on watershed management Vol. II. 21-23 July 1980. Boise, Idaho. Amer. Soc. Civil Engineers.

Doescher, P.S., R.F. Miller, and A.H. Winward. 1984. Soil chemical patterns under eastern Oregon plant communities dominated by big sagebrush. Soil Sci. Soc. Amer. J. 48:659-663.

Ganskopp, D.C. 1985. Success of broadcast seeding on untreated, imprinted and chained rangelands, p.4-6. In: 1985 Progress report...Research in Rangeland Management. Oregon Agricultural Exp. Stn. Spec. Rep. 743.

Goebel, C.J. 1978. Grass establishment on lower Snake River rangelands. p. 629-630. In: D. N. Hyder (ed.) Proceedings First International Rangeland Congress. 14-18 Aug. 1978, Denver, Colorado. Soc. for Range Management, Denver, Colorado.

Haferkamp, M.R., D.C. Ganskopp, R.F.Miller, and F.A. Sneva. 1987. Drilling versus imprinting for establishing crested wheatgrass in the northern Great Basin. J. Range Manage. (accepted 1987).

Haferkamp, M.R., R.F. Miller, and F.A. Sneva. 1985. Seeding rangelands with a land imprinter and rangeland drill in the Palouse Prairie and sagebrush-bunchgrass zone, p.19-22. In: 39th annual report, Vegetative rehabilitation & equipment workshop. 10-11 February 1985, Salt Lake City, Utah. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Hyder, D.N., and R.E. Bement. 1969. A micro-ridgeroller for seedbed modification. J. Range Manage. 22:54-56.

Hyder, D.N. and R.E. Bement. 1970. Soil physical conditions after plowing and packing of ridges. J. Range Manage. 23:289-292.

Hyder, D.N., D.E. Booster, F.A. Sneva, W.A. Sawyer, and J.B. Rodgers. 1961. Wheel-track planting on sagebrush-bunchgrass range. J. Range Manage. 14:220-224.

Hyder, D.N. and F.A. Sneva. 1956. Seed and plant-soil relations as affected by seedbed firmness on a sandy loam rangeland soil. Soil Sci. Soc. Amer. Proc. 20:416-419.

Hyder, D.N., F.A. Sneva, and W.A. Sawyer. 1955. Soil firming may improve range seeding operations. J. Range Manage. 8:159-163.

Klomp, C.J., and A.C. Hull, Jr. 1972. Methods for seeding three perennial wheatgrasses on cheatgrass ranges in southern Idaho. J. Range Manage. 25:266-268.

Larson, J.E. 1980. Revegetation equipment catalog. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Luke, F., and S.B. Monsen. 1984. Methods and costs for establishing shrubs on mined lands in southwestern Wyoming, p.286-292. In: Tiedemann, A.R., E.D. McArthur, H.C. Stutz, R. Stevens and K.L. Johnson (compilers) Proceedings--symposium on the biology of Atriplex and related chenopods. 2-6 May 1983, Provo, Utah. USDA Forest Service, Intermountain Forest and Range Experiment Station. Gen. Tech. Rep. INT-172.

Marlatt, W.E., and D.N. Hyder. 1970. Soil ridging for reduction of wind erosion from grass seedbeds. J. Range Manage. 23:170-174.

McGinnies, W.J. 1962. Effect of seedbed firming on the establishment of crested wheatgrass seedlings. J. Range Manage. 15:230-234.

Nelson, J.R., A.M. Wilson, and C.J. Goebel. 1970. Factors influencing broadcast seeding in bunchgrass range. J. Range Manage 23:163-170.

Tye, J. 1980. A rangeland renovation project in southwest Texas, p. 10-11. In: 34th annual report, Vegetative rehabilitation & equipment workshop. 10-11 February 1980, San Diego, California. USDA Forest Service, Equipment Development Center, Missoula, Montana.

Vallentine, J.F. 1980. Range development and improvements. Second edition. Brigham Young University Press, Provo, Utah. 545p.

IDENTIFICATION OF FUTURE RESEARCH

Gary R. Evans[1]

ABSTRACT

Future research directions must focus on under-
standing the mechanisms and processes of
secondary succession, both natural and manipu-
lated. Resource managers will need to understand
how to recruit and maintain desired seedlings in
the community by the most cost effective means
possible.

INTRODUCTION

To properly assess the future, one must be
capable of identifying and defining variables
which affect events or decisions to come, and
also determining the level of impact each
variable will have on causing the event or
decision to take place. If all variables are
precisely defined and the effect is fully
known, then we can say that the future event or
decision is known with perfect knowledge.
Should this occur, the event or decision will
probably already have taken place, since that
is the only way to have perfect knowledge.

It is, however, reasonable to assume that some
amount of unknown, i.e. partially defined
variables, and some level of risk must enter
into the perception of future events. Pursuing
a typology of decisions (fig. 1) to the polar
opposite of the theoretical state of perfect
knowledge, the problem becomes the inability to
identify all of the variables, much less
describe these variables. Since the variables
cannot be defined obviously, the ability to
assess the level of risk does not exist.

The two remaining components of the decision
typology represent the realm of events most
likely to be encountered in an assessment of
the future. The first of these components is
comprised of decisions where all variables are
known and reasonably well described and some
level of risk can be assigned to the effect of
the variable upon an event or decision. Events
that fall within this component are normally
those occurring in the near future. The other
component contains variables, not all of which
can be clearly identified or defined.
Therefore, the level of reliability or risk
assigned to these variables is relatively low.
Extending the previous logical argument implies
that this component describes events occurring
on time horizons far into the future.

The focus of this paper may be approached from
either of two alternatives. The first is to
identify future research in the near term (that

is in the next 1-3 years) or to identify
research much further into the future. This
paper will attempt to identify future research
on a much longer time horizon.

Areas for future research direction have been
part of the topics of discussion throughout
this symposium. As previously stated, however,
not all variables influencing the future are
now clearly discernable. The very nature of
this inability to clearly discern the future
implies change. The dynamics of change require
that continual reassessment of the state of a
system must occur. Furthermore, it is from
this continual re-evaluation of the moving
target of new knowledge that new goals and new
priorities emerge.

OBJECTIVE

This paper, by virtue of its place in the
proceedings is designated to bring cloture to
the symposium. It will also establish some new
goals and identify future opportunities.

The central theme of the symposium provides an
opening for stating some basic assumptions.
First, it has been the goal of all participants
to better understand the processes of
germination and mechanisms for establishment of
rangeland plants. Therefore, one must ask, "If
this knowledge has been improved, at what
price?" Second, having acknowledged that it is
desirable and beneficial to improve the process
of establishing rangeland plants, then the next
immediate question must be, "what have we
learned, how well are the mechanisms and
processes understood, and what is next?"

THE CHALLENGE

Range scientists and resource managers have
recently been challenged by some different
ideas and concepts which should firmly shake
the foundation of some long held and cherished
beliefs about management of renewable natural
resources, particularly in arid and semi-arid
environments. This challenge is legitimate,
valid, and timely, as is this symposium. Some
of today's answers, however, may not be fully
legitimate. Many data bases must be assessed,
sorting our myths, folk lore and empirical
wisdom from scientific fact. "What is not yet
known?" It is not my intention to denigrate
any concept of renewable resource management,
but rather to use the present challenge as a
torch, to set a fire under the collective seats
of learned knowledge.

The goal is to gaze into the future and
identify where science needs to go in search of
ways to improve the processes of secondary
succession on range and pasture lands in the
world. The scientist's challenge is to
approach the future with an open mind and
expanded vision and see where it leads.

---

[1]National Program Leader-Range, USDA-ARS,
Beltsville, MD 20705

Figure 1 (Evans 1976)

<u>Risk known</u>   <u>Risk unknown</u>

Variables-all known and described   Variables-all known, some not described
Risk-assigned perfectly   Risk-not all assigned

Variables-all known and described   Variables-known and not well described
          imperfectly   unknown, not described
Risk-known and assigned   Risk, not all assigned

SECONDARY SUCCESSION

The very theme of the symposium speaks to
secondary succession both naturally and
artificially induced. Many papers have focused
on artificially speeding up or significantly
altering the successional process, to achieve a
desired ecologic stage. In each and every
case, however, the papers have focused on
inducing establishment or mechanically
establishing seedlings of plant species desired
by renewable resource managers. It is a good
beginning. Without the knowledge gained to
date, it would not be possible to establish
challenges for the future.

FUTURE CHALLENGES

Scientists and resource managers must
understand the processes that support the
recruitment of seedlings into a plant community
either artificially induced or naturally
induced. It is necessary to unravel the
mechanisms that enable the process to take
place.

Range, and often much pasture land cannot pay
back, in increased quantity and quality of
desired plant species, the costs of extensive
revegetation practices. This is especially
true in today's market place. Managers must
better understand how to obtain desired species
and composition for the least cost. This will
require a clear description and understanding
of interactions involving the soil system with
the seed and seedling. The need for improved
knowledge is just as true for arid lands with
unpredictable precipitation as it is for
sub-humid lands with reasonably predictable
precipitation patterns. It is acknowledged,
however, that it is easier to get the job done
if there is more readily available effective
moisture. Yet nearly half of North America
including 80% of the range falls in the more
arid conditions.

The previous papers have presented many of the
complexities of the physical environment as
variables in the process of establishing an
adequate stand of desired vegetation. The
challenge now at hand is to translate knowledge
into the most economically efficient process
possible. Questions may include the
following: What are the quantifiable levels of
biological competition in the root zone and the

vadose zone that affect a seedling's success or
failure? What are the quantifiable mechanisms
that encourage or inhibit interspecific
competition between established plants and
seedlings; both at the soil surface and within
the root zone? What are the quantifiable
effects at the soil/seedling interface of
varying soil textures, varying moisture regimes
and varying levels of disturbance? What
biochemicals and forms of allelopathy are
beneficial or harmful to the processes of
secondary succession?

The point being illustrated by this series of
questions is that empirical descriptions of
what happens when a certain species or mix of
species is introduced to the community is no
longer enough. It is time to get down to
"brass tacks" to describe, define, and quantify
the mechanisms that enable the process of
secondary succession to take place. Bits and
pieces of the knowledge base exist. That is
clearly documented by the symposium.

Scientists conducting research in support of
renewable resource management can develop the
highest quality germplasm base for livestock
and wildlife to graze, and to protect the soil
resource, but if it is not utilized by the
resource manager then such work is of little
value. For example, ARS and many universities
have invested considerable money to understand
the problems of tall meadow fescue. Once these
problems were identified, that is endophyte
toxicosis and fescue foot, scientists set out
to conquer the problem. Out of this investment
arose endophyte-free fescue and the beautiful
hybrid <u>festuca-lolium</u> crosses, one of which is
now on the market as Johnstown fescue. Yet, in
the past year it was pointed out to the author
that what livestock producers in the infected
fescue area desired was a way to block the
toxic effects of fescue in cattle, horses and
sheep, not replace the problem vegetation.

There are many conclusions that may be drawn
from this illustration. However, the principal
point was, very clearly, the fact that the "new
stuff" would not establish as well, may not
compete as well, took too much management and
was an unknown as to how it would respond to
management, pests, etc. Furthermore, the cost
of reestablishing the high quality fescues was
prohibitive given current livestock markets.
The question is, what else must be understood
about the process of secondary succession to

economically modify the present vegetation.

The good news is that scientists are trying to understand and partly describe mechanisms and processes of secondary succession. The symposium is a good example. However, scientists are also faced with the need to deal with many grazing lands where revegetation costs are prohibitive or where socio-cultural conflicts are arising, such as, management of public lands.

Future research goals must focus on describing and quantifying the basic mechanisms of secondary succession. Developing a clear understanding by the scientist, will enable the resource manager, either livestock producer or range conservationist, to design management systems that enable nature to do more of the revegetation job.

Some of the areas that demand a better understanding are: interspecific competition between established perennial monocots and monocot seedlings; monocot and herbaceous or shrubby dicot interspecific competition with dicot seedlings; physical and biological factors affecting interspace areas in established communities of perennial plants; biotic impacts above and below ground of large fauna, i.e. insects and small mammals; genesis, function and effect of soil surface layering, pavement, and cryptogams; and many others.

Not only is it important to describe, quantitatively the processes influencing secondary succession, it is also equally important to develop mechanistic models capable of predicting responses when external variables cause changes to the biotic system or to predict responses when attempting to manage areas where data bases may not be available.

SUMMARY

The symposium represents the state of knowledge about seed and seedbed ecology with particular emphasis on the western, and the semi-arid, ecosystems of the U.S. This collective work represents an excellent beginning in understanding two major parts of the process of secondary succession, both natural and induced; that of seed germination and seedling development. The challenge for the future is to describe how these two components function in the ecosystem, the "whole system;" to learn how the small, weak and very vulnerable biological entity (the seedling) can effectively compete and survive in the system and at the same time recruit additional seedlings. The window of knowledge has been slightly opened, the work is just beginning.

LITERATURE CITED

Evans, Gary R. 1976. Role of resource planner in quantitative choice making. Ph.D. Thesis. Colorado State University. 146 pp.